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THE JOURNAL  
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Comparative Neurology.

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A QUARTERLY PERIODICAL  
DEVOTED TO THE  
Comparative Study of the Nervous System.

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EDITED BY  
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# CONTRIBUTIONS TO THE COMPARATIVE MORPHOLOGY OF THE CENTRAL NERVOUS SYSTEM.

## I.—ILLUSTRATIONS OF THE ARCHITECTONIC OF THE CEREBELLUM.—Plates I-IV.

C. L. HERRICK.

Aside from the physiological questions offered by the encephalon, which are confessedly among the most difficult of neurology, there are many more general problems respecting the principle and details of construction, relation to other parts of the central organ, and histogenesis, which are very far from a satisfactory solution. Even those points which can be accepted as well settled require concrete illustration to make them available for purposes of instruction. In the following notes it will not be necessary to sharply define that part which is regarded as a new contribution to our knowledge from the points for which the more general utility is hoped, since all the statements are equally the result of direct observation and are quite independent of the work of others.

It is hoped that the comparison of the several groups of vertebrates and identification of the close correspondence between the respective adult conditions of the organ and the transitory stages in the mammalian cerebellum during its development may add force to the plea for more complete application of this comparative method to the study of neurological problems.

Like all other organs arising from the walls of the embryonic vesicles, the cerebellum can be traced primarily to a more or less distinctly circumscribed area of this wall; and its subsequent modifications consist, in part, of irregularly distributed increase in size accompanied by rapid multiplication of cells, and, in part, of folds and contortions in the resulting structure.

The several processes concerned in the development are briefly outlined by Mihalkovics,<sup>(1)</sup> rendering it unnecessary to do more than briefly recapitulate the processes.

Fig. 2 of Plate II is a camera drawing of an exactly median section through the brain of a guinea-pig before the cerebellum has at all differentiated from the cephalic portion of the dorsal wall of the nerve-tube. The transition caudad into the velum medulare posterior (v. p.) is gradual, and the latter shows very little tendency to fold upon itself, as it will soon do in the formation of the metaplexus. Fig. 3 is a similar section, though not strictly median, of a later stage in the mouse embryo. Here the velum has sharply folded and the plexus is very rapidly forming by a succession of inward folds, as a result of which the original epithelium of the roof of the fourth ventricle is converted into the epithelium of the plexus. The cerebellum itself exhibits a decided tendency to a forward (cephalad) fold, and the whole organ may be readily compared with that of amphibia or lower reptilia.

It will be specially observed that the dorsal surface is devoid of cells and contains a rudimentary superficial tract. This condition is the permanent one in reptiles like the turtles. Compare Plate III, Figs. 4, 5 and 6, with the above mentioned. In the case of the turtle, *Aspidonectes spinifer*, as there figured, the basal portion of the cerebellum is perpendicular to the axis, the dorsal portion being twice flexed, with a slight tendency to recurve at the tips. The specimen

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<sup>1</sup> MIHALKOVICS, "Entwicklungsgeschichte des Gehirns, nach Untersuchungen an höheren Wirbelthieren."



figured being very young, it cannot be supposed that these folds have been completed. The pons flexure has been considerable, bringing the extremity of the cerebellum caudad into proximity to the obex and taeniæ fossæ rhomboid-ealis. The velum medullare posterior is therefore almost wholly converted into the epithelium of the metaplexus. The entire configuration of the cerebellum is hood-like (Plate III, Figs. 9, 10 and 11).

In the black-snake the cerebellum is a leaf-like expansion, having on the caudad surface (really the ventral or ventricular aspect) the granular substance and the white fibrous zone cephalad; but this leaf is folded ventro-caudad, so that the white layer is dorsad and uppermost and the gray matter faces toward the ventricle in which lies the large plexus.

In the case of the lizard we have apparently a completely dissimilar plan of structure. Here the gray matter is dorsal and the white ventral (Plate IV, Figs. 4 and 5). This reversal of the two layers is explained, upon a more careful examination, as the product of a complete forward and median fold of the caudad and lateral margins of the cerebellum. (Compare Plate IV, Figs. 6-9). This is but the completion of the process indicated by the incipient retroflexion seen in the turtle. The result of this fold is the formation of an actual cavity surrounded caudad and laterad by the white (morphologically dorsal) zone of the cerebellum. Thus the fusion of the lateral margins, or, more accurately, the union of the whole latero-caudad reflected margins due to a general cephalo-median increase, produces the hollow organ just described.

In the alligator the cerebellum is formed in the same way, but the organ is larger and the internal secondary cavity is much greater, the whole forming a cone with its apex protruding caudad. In this case the folded portion has undergone less flattening dorso-ventrally, and more clearly

illustrates the nature of the processes to which its formation is due.

It seems at first sight quite out of the question to expect to find any homologous processes in the brain of the higher vertebrates. In the first place, the relation between the Purkinje cells and the granular zone (molecular layer) is not the same, and, in the second place, there seems to be no evidence that such a wholesale revolution has taken place; but, on the other hand, very sufficient evidence that the increase in surface has been effected by a different plan, *i.e.*, the corrugation of an organ, which increases in thickness rather than length. It is true that in birds there is an obvious partial revolution of the whole cerebellum through a considerable arc, but this is more easily explained by reference to the flexures incident to the great compactness of the avian brain and the freedom of rotation due to the extensive development of the velum medullare anterior, which leaves the cerebellum quite disassociated from the corpus posterior and free to rotate upon the peduncles as a lateral horizontal axis.

Among mammalia, the cerebellum of the opossum indicates a decided tendency to revolution from behind cephalad. Of the several primary convolutions first formed, the posterior continues growth longest and eventually circumscribes the anterior, and, with its secondary gyri, forms the ectal surface, as may be readily seen in longitudinal sections. One additional consideration may, nevertheless, lead to a prosecution of a search for some plan of revolution or evagination in the mammalian cerebellum as well as in the reptilia. It is this: if the conclusions of His and others regarding the typical histogenesis of nervous and connective elements in the nerve-tube be correct, it is difficult to understand the origin of the cells of the cerebellum by reference to the adult relations. We have the ventricular surface lined with the usual epithelium, which is, during an early period, proliferous, as may be easily demonstrated.



But the area of ventricular surface is progressively restricted until it is reduced to insignificance, and can be brought into no relation with the Deiters and Purkinje cell-layers. His<sup>(1)</sup> concludes that the nervous elements have arisen by a subdivision of certain of the nuclei of the epithelium near the ventricular wall and thence migrate to their definitive foci. Such a direct migration is rendered impossible in the present case by the early development of the central tract of white matter.

Again, it is a fact of observation that at a period not long before birth in rodents, for example, the surface of the cerebellum ectad to the Purkinje cells, which are already present, is covered by a thin zone of rapidly dividing cells, which, as they increase, are also passing entad, to a level beneath the cells of Purkinje.

This remarkable assemblage of superficial cells with dividing nuclei, caryokinetic figures and other evidences of proliferation may be readily seen in the cerebellum of old embryos of the guinea-pig (Plate II, Fig. 4, and Plate I, Fig. 9). The condition indicated in Fig. 9, where the corpuscles are much more numerous superficially and are there more frequently dividing than in the infraganglionic zone which is their ultimate locus, and the fact that the superficial proliferating zone almost entirely disappears in the adult sufficiently shows that these cells are not indigenous, and suggests the necessity of tracing the history of the proliferating zone. That this zone does not arise *in situ* is rendered somewhat probable by the fact that no such layer exists in reptilia, but the ventricular surface is the proliferous locus, even though in the higher reptiles it is reverted so as to become spuriously ectal in position. On the other hand, it would at first appear that we have a case quite comparable to the present one in the cerebrum where the cells of the cortex proliferate at the surface and migrate to their various

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<sup>1</sup> Wm. His, Archiv f. Anatomie u. Physiologie, Anatomische Abtheilung, 1890, p. 95 et seq.

positions, as may be gathered from sections of earlier embryos than that figured on Plate II, Fig. 4. It may be remarked in passing that, in our opinion, the latter analogy is misleading, since, as we shall hope to show, the proliferating centres from which the cortical cells are derived are central or ental rather than superficial. The solution of the problem of the histogenesis of the cerebellum is to be sought in earliest stages of its development, which can be shown to follow in a condensed manner the course just indicated for reptiles.

Returning now to the embryo mammal (Fig. 2, Plate III) and again noticing that the dorsal surface is devoid of cells except at the caudad extremity, we observe that in an older embryo (Fig. 3) a much larger portion of the dorsal surface has been thus covered, and evidently from behind forward. Fig. 1, which is a transverse section through one-half the cerebellum near its base and part of the medulla in a mouse embryo of a little older stage, shows that the entire surface has now been covered by the proliferous zone, but that it is curiously double, with a layer of white fibres separating the two zones. It is also observed that the walls of the nerve-tube at the recessus lateralis of the fourth ventricle are very thin, and consist of very rapidly proliferating and hence closely-packed cells which pass from the ental to the ectal surface. This section suggests that possibly the lateral (and caudad) portions of the ventricular surface of the cerebellum may be the sources of the proliferating superficial layer of the dorsum. Yet we have no clue to the double character of this proliferous zone, and have no direct proof that the suggestion is valid. Before we can secure such proof it will be necessary to thoroughly understand the nature of these lateral recesses of the fourth ventricle. The description given by Mihalkovics, though incomplete, is very suggestive:

Bemerkenswerth von der Seitentasche [*Recessus lateralis*] ist, dass sie im ausgebildeten menschlichen Gehirn aus zwei einander berühr-

enden Blättern besteht; das obere Blatt liegt dem Wurzeltheil des Kleinhirns, das untere dem verlängerten Mark an. An günstigen Objecten nach Alcohol-erhärtung ist beim Abheben des Kleinhirns von der Medulla gut zu sehen, dass die scheinbar aus einer Lamelle bestehende Seitentasche sich öffnet und das Gange einer Blase gleich sieht. Ich finde also Henle's Bemerkung dass das *velum medullare inferius*, wie er die Seitentasche nennt, manchmal den Eindruck einer collabirten Blase macht, ganz zutreffend, obgleich er die zwei Blätter der Blase nicht erwähnt.

Diese letzteren entstanden dadurch, dass die Seitentasche im embryo blasenförmige Gebilde resp. die vorgestülpten Seitentheile der hinteren Deckplatte waren, welche mit der starken Ausbildung der Kleinhirnhemisphären in den Winkel zwischen Kleinhirn und verlängertes Mark eingeknickt und plattgedrückt wurden.

Das obere Blatt der plattgedrückten Blase, welches mit der *lamina basilaris* (Aeby) des Kleinhirns in Berührung steht, ist bedeutend schwächer als das untere, und mit der Pia-hülle in festem Zusammenhang — es tritt an dasselbe ein Zug von feinen Adergeflechtzotten vom Plexus choroid. ventr. IV. zum gleich zu schildernden Blumen-Körbchen. Mit dem starken unteren Blatt der Tasche sind die Wurzelfasern des N. glossopharyngeus und Vagus verwachsen. Die Taschen sind also Mark-lamellen in welchen die nervösen Elemente nicht ganz schwinden; sie sind rudimentäre, nervöse Gebilde, wie die Nervensäume (*taeniae medullare*) am Rande der Rautengrube. Gleiche wie jene sind die Taschen mehr oder weniger ausgebildet, entsprechend der schwächeren oder stärkeren Involution der nervöse Elemente.<sup>(1)</sup>

The passage quoted above gives a clear idea of the origin of the *recessus lateralis*, but fails utterly to suggest any cause or purpose for such a peculiar involution. Of course, it might be regarded as a necessary mechanical concomitant of the increase in growth of the cerebellum and the several changes of position which that organ suffers during its development as a result of the flexures of the brain axis and corrugations and convolutions of its roof. It can, in fact, be seen that the *metaplexus* and its lateral projections, known as the *cornucopiae* (Blumenkörbchen), stand in intimate relation to the lateral chambers, and that the development of the *eminentia acustica* may also sustain a more or less direct relation to these cavities, but the real *raison de etre* must be sought in the histogenetic necessities of the cere-

1 MIHALKOVICS, *Entwicklung des Gehirns*, p. 5-8.



bellum itself, while these, in turn, can be traced to the progressive metamorphosis of the primitive lamella, of which the vertebrate cerebellum is the final product. A reference to Plate I, Figs. 3-8, will place all these relations in a clear light. These sections through the cerebellum and medulla of a guinea-pig exhibit the same process of lateral and retorse growth and folding which are seen in reptilia, except that, instead of the flexion of the entire organ, there is a comparatively thin fold of epithelium containing a delicate tract at the base, but consisting caudad solely of the epithelium. These sections taken through the same cerebellum at different points may fairly claim to indicate the several stages which would successively appear at any one plane.

Fig. 3, taken through the base of the cerebellum, shows the dorsal surface to be devoid of the gray matter. From either side there extends a curious upward fold containing a cavity. The source of the growth is evidently the walls of the cavity, as witness the numerous cells clustered at that point. Fig. 4 shows the circumscribed cavity to be a pouch of the recessus lateralis of ventr. IV, extending cephalad, and also shows that the newly-formed cells involved in the fold are driven from the ventricular epithelium. It will be noticed also that the entire dorsal portion of the organ is affected by this overlapping growth from behind and the sides, so that a groove is formed on either side meson, dorsally. It is likewise important to observe that the development of the epithelium extends the recessus lateralis ventrally as well as dorsally, and that it there also fuses with the entad body (here medulla) and gives rise to proliferous clusters.

The above illustrations are derived from the guinea-pig, but figures are also given derived from similar sections of older stages of mouse embryos for demonstration of the last-mentioned point. In these cases the dorso-lateral fold has already fused with the walls of the cerebellum, and the

cavity has nearly disappeared. Fig. 7 well exhibits the extent to which the gray matter of the dorso-lateral aspects of the medulla is derived from the epithelium of the primitive recessus lateralis. Fig. 8 illustrates the method of plexus formation, the origin of the cornucopia, and conditions prevailing at the tip of the cerebellum at this stage.

The origin of Purkinje's cells cannot be fully made out in this series, yet the great similarity to the cells of the dentate nidulus, at a stage shortly preceding birth, is such as to suggest community of origin.

Additional evidence that the principle formulated above is the prevailing one has been derived from a study of embryos of the black-snake (see plate X). While in this case the organ does not itself undergo retroflexion, but remains a leaf-like organ, longitudinal sections indicate that proliferation is most rapid near the tip, and a dense cluster of cells is pushed dorsad and then cephalad upon dorsal surface. This does not exclude direct migration from the ventricular aspect of the cerebellum. There is every reason to conclude from these sections that the cells of Purkinje likewise spring from near the ventricular border. At the tip and lateral margins, the layer of these cells in the embryo comes in contact with the epithelium, and the cells, which are obviously multiplying rapidly, either spring from the epithelium by subdivision of its undifferentiated cells or the multiplication of special germination cells. The neuroblasts at first become spindle-shaped and give rise to a process which passes cephalad (Plate X, Fig. 11). Nearer the base the layer of Purkinje cells is represented by a thick nucleary zone from the epithelium. At the very base, however, there is a superficial (dorsad) cell aggregate which likewise seems to have its origin in the epithelium of the ventricle.

It seems unnecessary to say more in illustration of the complete homology between the method of cerebellum formation in the several groups of vertebrates. That this

development corresponds to the course of evolution as deduced from the adult conditions of various reptiles seems equally clear, and the whole argument forms a beautiful illustration of the interdependence of all biological sciences.<sup>(1)</sup>

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## II.—TOPOGRAPHY AND HISTOLOGY OF THE BRAIN OF CERTAIN REPTILES.

*Materials.*—The brief notes here following, like the first paper of the series, published in the *Journal of the Cincinnati Society of Natural History* for 1890, are to be regarded as materials for elaboration in a more systematic way when they shall have accumulated sufficiently to make such systematic treatment profitable. The present instalment deals primarily with the prosencephalon, especially the distribution of its cells and commissures. The materials consist of a number of brains of the small lizard *Sceloporus undulatus*, locally abundant in Scioto county, adult and embryonic brains of the black-snake, and a specimen of the turtle, *Aspionectes spinifer*.

*Topography and external form of the lizard brain.*—The form of each hemisphere is, roughly speaking and exclusive of the elongate olfactory lobe, a triangular pyramid. In horizontal section the angle formed by the median and caudad planes bounding the hemisphere is about 120°. The third side is a gentle curve more rapidly arching to the cephalad extremity. The diencephalon is included within the reëntrant angle formed by the caudad planes of the two hemispheres, for externally the latero-caudad angle of the hemisphere is in contact with the cephalo-lateral projection

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1 The close approach made by Obersteiner to the view here announced is indicated by the following quotation from Meynert, *Psychiatry*, p. 116:

"According to Obersteiner, the cerebellar cortex in the child is covered by a layer of formative cells, which are transformed into spindle-shaped fibrils, thus constituting an innermost stratum of the pia mater."



of the optic lobes, the horizontal section of which is triangular in the opposite sense to that of the hemispheres.

The base (ventral surface) of the hemispheres exhibits a slight protuberance in the latero-caudad portion, which is due to the protrusion of the *occipito-basal lobe*.<sup>(1)</sup> The latter is not a subdivision of the cortex, but a well-defined portion of the axial lobe, in the sense elsewhere employed. This lobe can probably be distinguished in all Sauropsida. It is partially separated from the remainder of the axial lobe by a fibre tract, and bears laterad and dorsad a film of cortex which projects caudad as a free *occipital lobe* of cortex for a short distance and terminates in a *velum cerebri*. The latter is morphologically a part of the wall of the lateral ventricle, which has here lost its cellular elements and contains at one point the *tænia thalami*.

The extent to which this lobe is developed varies greatly even in reptiles. It is reduced to a minimum in birds. It contains the undoubted homologue of the hippocampus, but in the black-snake that portion homologous with the hippocampus is relatively highly differentiated. Even the portions corresponding in cellular structure to the fornicate and uncinatè gyri may be distinguished, though there is, of course, no external indication of this distinction. The terminal, caudad portion (homologue of the uncinatè gyrus) contains densely packed fusiform cells of relatively small size, while, near the juncture of the free portion with the axial lobe laterad, there is a larger area containing much larger cells of the same type, which corresponds with the fornicate gyrus of mammals (Plate X, Fig. 6). At some levels a deep depression separates the hippocampus from the remainder of the cortex.

Ventrally the occipito-basal lobe is set off from the axial lobe proper by the pyramidal tracts, and is filled with small

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<sup>1</sup> The use of the word "lobe" in this and subsequent cases is a pure convention, from which no escape could be found. "Region" might be a preferable term, if not too vague.

multipolar cells resembling those of the second olfactory or rhinomorph type, not exceeding .010 mm. in greatest diameter.

The occipito-basal lobe in the black-snake is much more complicated, and, in order to understand it, a description of the topography of the entire cerebrum may be necessary. The hemispheres are strongly protuberant and abbreviated. The cephalad portion is suddenly constricted and applied laterad to the apparent crus of the olfactory, so that a considerable portion of the cortex actually extends out upon the olfactory lobe. The olfactory structures proper accumulate at the mesad surface, where they are strongly developed, while the laterad portions cephalad are reduced to a thin film of fibres. The result of this peculiar limitation is that the large olfactory ventricle curves laterad from the base to near the tip, where it abruptly arches mesad, so that the olfactory fibres take their origin from the mesal surface, toward which the glomerular layer presents a concavity for their reception (Cf. Plate X, Fig. 6).

The concentration of the cortex caudad accounts, partly at least, for much that here follows. The ventro-basal protuberance of the hemispheres, which seems analogous in position to the pyriform lobe of Rodents, for example, contains a concentric zone or hollow spheroid of gray matter greatly (though spuriously) resembling the hippocampus. This concentric mass of cells, which makes up the major portion of the occipito-basal lobe, contains fusiform cells which in some places are rapidly proliferating. Cephalad to it lies a dense cell-mass representing the central division of the axial lobe. Dorsally the concentric caudad portion becomes quite distinct from the non-concentric cephalad body. There is also a small latero-caudad cluster ectad to the occipito-basal lobe, and it, like the ventral and cephalad parts of the central lobe, contains pyramidal cells predominately.

In the lizard a tract can be traced to the region of the

occipito-basal lobe from the diencephalon, entering dorsad to the peduncles. If correctly followed, these fibres have their origin in dense cell-masses near the middle of the thalamus at about the level of the dorsal part of the anterior commissure.

A distinct bundle from the anterior commissure may be traced to this lobe, though its exact destination is not known. But, inasmuch as the tract can be followed to the median part of the lobe and a well-defined nidulus<sup>(1)</sup> lies in their course produced caudad and laterad, it is natural to conclude that the two are related.

This *occipito-basal nidulus* is not a single cell cluster, though it contains a central aggregate which is sharply defined. A short distance dorsad to the ventro-basal protuberance of this lobe a few rather large fusiform cells with large pale nuclei appear in clusters along the caudad border of the lobe. These become more numerous in regions farther dorsad and accumulate in small clusters, which fuse at a level somewhat dorsad to the anterior commissure to form the axial nidulus of the lobe above referred to. Such nests or aggregates seem to be a constant feature in all reptilia. We have observed them in the Chelonia, Ophidia, and Sauria (see notes upon the brain of the alligator, Plate VII, Figs. 7 and 8). Mr. Turner finds similar proliferating areas in the corresponding region in birds.

In the black-snake a distinct fibre-tract from the caudad strands of the anterior commissure passes to the caudad or ventricular surface of this lobe and passes to its laterad portion. The cells of the lobe in this case are beautiful illustrations of flask cells with apical processes chiefly median.

In the *frog* the occipito-basal lobe is well developed, but is very simply constructed, consisting of numerous more or less concentrically arranged flask cells with fibres passing

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1 A substitute for the word "nucleus" as applied to central cell clusters.



caudad and entering the thalamus from the caudo-lateral aspect of the ventral part of the hemisphere. This tract doubtless corresponds to the direct thalamus tract noticed in the lizard.

In horizontal sections of the ventral part of the hemisphere in the *lizard* a large central mass can be distinguished, which, although it may contain homologues of part, at least, of the striatum, may here be called simply *central lobe*. It receives the pyramidal tracts.

There is ectad to this a lenticular gray mass, with few or inconspicuous cells, which is separated both from the lateral cortex and the central lobe by fibre-tracts. There is a certain resemblance to the claustrum, though no such homology is suggested for what may be termed the *lenticular nidulus*. Peripherad to this nidulus is the narrow *parieto-frontal* lobe of the cortex, with its densely-packed pyramidal cells.

Further cephalad and dorsad a small triangular cluster, apparently connected with the lenticular nidulus, reaches the surface, forming a *frontal lobe*. Still further dorsad a small oblique and very dense lamina of closely-packed cells of the flask variety appears. This is the most conspicuous of all the lobes in section, and may be termed the *fronto-median* lobe. In transverse sections the fronto-median lobe appears as a very densely cellular band of nearly uniform width, occupying the middle of the width of the tectum cerebri, and separated from the ventricle by the tracts passing cephalo-dorsad from the callosum via the intra-ventricular lobe. There are very evident connective fibres springing from the ventricular epithelium and passing through the callosal tract toward the surface at the median fissure. Upon these fibres are the usual "glia" corpuscles, with elongate outlines and granular texture. The cells of the fronto-median lobe are fusiform elements of the sensory type, except cephalad, where there is an admixture of the deeply staining pyramidal variety. The contrast between these cells and those of the frontal lobe is very striking.

The *intra-ventricular lobe*, or that portion mesad of the lateral ventricle, becomes quite distinct dorsad by the separation from the thalamus and backward extension of the ventricle. It is filled with irregularly dispersed flask cells, and also contains the cephalo-dorsad prolongations of the callosal tracts. The finer structure of the intraventricular lobes may be gathered from the figures (Plate II, Fig. 16, and Plate IV, Fig. 8). The portion drawn in Fig. 8 is from that part of the lobe near the ventricle of the right hemisphere. The epithelium of the ventricle is produced, as usual, into long connective fibres, which do not appear in the figure because the section is oblique to their axes. The entire lobe is filled with bipolar or multipolar cells, with the large reticular nuclei and generally fusiform contours of æsthesodic cells. The fibres do not preserve any definite direction, but the long axis of most of the cells lies in the horizontal plane and prevailingly in the cephalo-caudad direction, while a smaller number extend perpendicularly or obliquely. The drawing was made under a one-fifteenth inch objective, with the aid of approximate micrometer measurements.

The course of the fibres of the callosum may be traced in transverse sections. At the point of crossing, the intra-ventricular lobe fuses with the thalamus, but cephalad the callosal fibres pass through that lobe dorso-cephalad until part of them pass dorsally to the ental aspect of the fronto-median lobe (*i.e.*, to the ventricular side) and thence to the dorsal cortex.

Medianly and ventrally the intra-ventricular lobe passes into that part of the axial lobe cephalad to the chiasm.

In higher sections the fronto-median lobe extends caudad and overlaps the intra-ventricular lobe on the median aspect. In the meantime the free caudad margin of the cortex has extended medianly, receiving the tænia from the habena and then fusing with the intra-ventricular lobe, and ultimately uniting with the fronto-median, completing

a ring or cap of cortex which entirely encloses the axial lobe, which latter, by the encroachments of the ventricle, has become separate from the walls. The cells of the occipital cortex resemble those of the fronto-median lobe (see Fig. 5 B, Plate III).

As already stated, the fronto-median and occipito-basal lobes become continuous toward the dorsum by circumscribing the intra-ventricular, which soon disappears. The result of the concrescence of the two areas and their subsequent increase in size is that nearly the caudo-median half of the dorsal cortex is covered by the flask, or sensory type of cells.

The caudad portion of the lateral cortex is considerably thickened, forming a distinct *parietal lobe*, of which the cells seem to be pyramidal or multipolar and stain deeply.

The intra-ventricular lobe is also quite prominent in the *frog*, forming a decided protuberance into the ventricle, and consists of cells of the type having large clear nuclei and fusiform outlines. Whether the function of these cells can be safely predicated from their form may well be doubted, but this much is certain, that these cells differ obviously from those of the lateral aspects of the cerebrum.

The fusion of the olfactory lobes with the cephalad part of the hemispheres somewhat disturbs the arrangement, but one may perhaps identify the homologue of the fronto-median lobe in an anterior projection into the ventricle, which is distinct from that just described, though filled with similar cells.

On the lateral aspect, the middle of the hemispheres exhibit a series of concentrically arranged cells near the ventricle and scarce and scattered pyramids in the ectal portions of the mantle. Cephalad there is a distinct nidulus ectad to the base of the olfactory protuberance. The cells of this nidulus are rather flask-shaped than pyramidal.

At higher (more dorsal) levels the occipito-basal and fronto-median lobes fuse through the mediation of the in-



tra-ventricular lobe, forming a continuous band, as in the lizard.

The whole lateral and latero-cephalad aspect of the hemispheres, on the other hand, is filled, dorsad to the base of the olfactory, with cells of a different type. They have the smaller nuclei and often the pyramidal form and deeper staining of the motor cells. It is true that these distinctions are rather less marked in the frog than in higher vertebrates, but they are perfectly obvious. These cells are also arranged in concentric bands, especially entally

A very large nidulus of small cells occupies the median portion of each hemisphere dorsad to the anterior commissure. It corresponds to the nidulus found in reptiles ventrad to the corpus callosum, but is very large.

It will not be attempted to homologize the axial lobe and its derivatives with the striatum of mammals, as several considerations seem to forbid a strict comparison. While there can be no doubt that the several divisions of the axial lobe contain the representatives of the striatum, yet there is no such sharp localization of areas nor differentiation of function as that seen in mammals. The cells of the central part of the cerebrum seem to be of the most generalized type, and, as I suggested in an earlier paper<sup>(1)</sup> there seems to be good ground for assuming that there are distinct centres of proliferation in these regions. Observations recently made on embryonic brains of rodents seem to indicate that there are such distinct proliferating centres in the cerebrum of mammals from which cortex cells are derived. A closer connection between the so-called Deiter or nutritive cell and neuroblasts than hitherto suspected may be suggested, as well as the possibility that the so-called basal ganglia are chiefly proliferating and trophic centres. Mr. Turner has arrived at the same conclusion respecting the basal ganglia in birds.

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1 "Notes on the Brain of the Alligator," *Journal Cincinnati Soc. Nat. Hist.*, 1890

as will be seen by reference to his paper elsewhere in this fasciculus.

#### FIBRE-TRACTS OF THE CEREBRUM.

Sections near the ventral surface of the cerebrum of the lizard exhibit the numerous fibres radiating rather uniformly cephalad and laterad from the cephalad extremity of the ventral peduncular tracts. A strong portion passes directly laterad, separating the gray matter of the occipito-basal lobe completely from the remainder of the section. This tract passes to the surface and is distributed by a number of branches in the cortical region, dorso-cephalad of its apparent destination.

Dorsad to this corona radiata the whole base of the cerebrum becomes filled with cells differentiating dorsad into the niduli already described. A rather distinct tract separates the intra-ventricular lobe from the frontal. This can be traced backward to the corpus callosum, which consists of few dark fibres passing from one intra-ventricular lobe to the other by a sharp caudo-ventral curvature.

As already stated, a very dense nidulus occupies the terma caudo-ventral to the callosum. The cells composing it are small, and, as only the nuclei stain, present the appearance of Deiter's corpuscles. Beneath the anterior commissure in the lizard is a similar dense cluster, which forms the only obvious demarkation between the prosencephalon and diencephalon. The tracts in the frog are as in reptiles. The tania thalami can be traced with perfect ease from the habena to the occipito-basal lobe, as also the fibres of the anterior commissure. The origin of the descending fornix fibres from the lateral extremities of the anterior commissure is likewise as in reptiles.

*Præcommissura.*—In the lizard it is rather difficult to trace the relation of the olfactory tracts and the præcommissura, because of the vertical height of the brain and the inferior olfactory development. Nevertheless, a distinct ven-

tral band of the anterior commissure can here be traced ventrad and cephalad. In longitudinal sections an olfactory tract lying medianly from the ventricle can be followed caudad and laterad to nearly the point at which the above-mentioned portion of the anterior commissure disappears.

In the black-snake, on the other hand, the anterior commissure is studied with great ease, and it exhibits greater complication of structure than in other reptiles examined (Plate X, Fig. 7). The commissure is readily separated into three perfectly distinct portions or bundles. The most ventral or ventro-cephalad bundle is the olfactory commissure, which is composed of large and deeply-stained fibres arching ventrad very soon after crossing to the opposite side and continuing almost directly ventrad to near the surface. They then turn cephalad and enter the medi-basal part of the crus olfactorius.

The second bundle (commissure of olfactory centres) lies in contact with the olfactory commissure and follows its course for some distance ventral, dividing into several distinct bundles of small size, which pass to the ventro-lateral regions of the middle portion of the hemispheres. These various bundles seem to enter cellular masses lying near the ventral and ventro-lateral surfaces of the cerebrum, and can be traced no further. A strong ecto-lateral tract from the olfactory lies superficially to these niduli, which are composed of small, dark, angular cells similar to those which in other animals are associated with the olfactory regions of the cortex.

The relations so far described are in no way conjectural, none of the fibres decussate, nor is there any connection between the olfactory commissure and the commissure of the olfactory centres. It might be supposed that the two tracts form a circuit broken by cellular matter in the olfactory lobes and again by the cells of the olfactory centres.

The third set of fibres lies dorsad to those just described,



and its fibres are not deeply stained, being perfectly distinct from both the preceding. They pass caudo-laterad and somewhat dorsad to the occipito-basal lobes, forming a tract along the caudad margin of the latter and arching over the peduncular tracts. It is from the lateral portion of this tract that the tracts apparently homologous with the descending pillars of the fornix arise. These fibres doubtless spring from the occipito-basal lobe and divaricate from the commissure of those lobes and then pass entad to the peduncles in their course to the homologue of the mammillare.

It will be seen that the fornix is a much more simple body than in higher vertebrates. Instead of two distinct portions with a cellular mass interposed near the median line, we have a continuous tract on either side from the occipital region to the mammillare. The nature of the tract ascending from the ventro-basal region to beneath the callosum in the alligator is left doubtful.

The complete differentiation of the commissural system in serpents is no doubt due to the great comparative complexity of the brain as a whole, and especially of the occipito-basal lobe and the greater extent of the free occipital cortex.

It should be added that the above description of the course pursued by the several branches of the anterior commissure leaves much to be desired as to the exact connections in the olfactory. There is, as already stated, a large mass of cortex upon the lateral and dorsal parts of the olfactory crus. It is from this that the strong latero-ventral tract originates, which then passes caudad, laterad, and dorsad beneath the cortex to a point as far caudad as the termination of the middle præcommissural tract. There seems to be no direct connection with the last named or the peduncular bundles. It also appears that the cephalad branch of the anterior commissure enters the cortex of the crus rather than the specific olfactory substance. The only

tracts from the latter seem to be short superficial ventral bundles, and, less certainly, a few median strands along the longitudinal fissure. We have much evidence that a similar condition prevails in mammals. The question also rises whether the caudad præcommissural tract be not homologous with the fornix.

The connective elements of the cerebrum have been variously interpreted, and chemical researches more refined than now possible may be necessary to fully discriminate the tissues. Our sections reveal two apparently distinct systems. The framework consists of the epithelium of the ventricles and their derivatives, the latter being in the form of fibres extending to the periphery and bearing at intervals fusiform inoblastic cells. The intervals left between these fibres is filled with a material which after treatment with acid and alcohol is reticular, and forms a mat or felt of great uniformity supporting the cells. As to the normal condition of this stroma, two views are possible, either the substance is composed of a reticulum and a soluble or coagulable filling, or the reticular appearance is artificial and the result of the partial solution and partial coagulation of what was originally a gelatinous and homogeneous mass. The latter view seems the more probable. Aside from the nerve cells, nutritive bodies having the appearance of migrant blood corpuscles are scattered in the stroma. These have only the nucleus colored, while the body is either dissolved or entirely transparent.

There is no marked difference in structure between the connective tissue of the cerebrum and that of the rest of the brain.

*The Diencephalon.*—The habena in the lizard forms a considerable cephalo-dorsal protuberance, consisting of two closely-packed cell-masses on either side of the cylindrical crus of the epiphysis. The two portions are connected by a small but distinct commisural band, which may be termed *commissura habenaria*. In the habena itself there are, in

addition to the prevailing fusiform cells with pale nuclei, many small dark nuclei, probably representing cellular elements like those of the granular layer of the cerebellum. The commissure does not seem like a decussation, and, although it may sustain some relation to the conarium, reveals none. Its convexity is caudad and dorsad, and its tracts pass latero-ventrad until they approximate to the optic tracts. It is impossible to determine at present whether they fuse with the optic tract or cross into the ventral part of the occipito-basal lobe. This tract comes into close relation with the superior commissure tract, or *tænia thalami*, but does not seem to fuse with it. We have here the solution of the relations which puzzled Osborn and myself in amphibia and the alligator. Instead of a division of the superior commissure we have to recognize two originally distinct commissures. The *commissura habenaria* seems to receive numerous fibres from the habena at a lower level.

The *supra-commissura* lies entirely cephalad to the habena at a level considerably ventrad to commissure of the habena (which lies caudad to it), and passes by a slight ventral curvature into the median part of the medio-caudad projection of the cortex, and thence across to the caudo-lateral portion. The superior commissure is relatively stronger than its neighbor, and it would appear that the two are especially distinct in animals like the lizard, where the epiphysis is highly developed.

If the superior projecting portion of the habena surrounding the base of the stalk of the epiphysis be considered the habena proper, the deeper and more ventro-caudad portion may be distinguished as the *nidulus* of Meynert's bundle or *nidulus Meynerti*. The fibres of Meynert can be traced to the portion mentioned (which in the black snake forms a distinct *nidulus*). The cells are rather larger than those of the habena, and less compactly clustered about the walls of the fourth ventricle extending some distance ventrad.



It seems probable that the projecting portion of the habenula has been frequently mistaken for the epiphysis. The plexus chorioideus which protrudes, and the fillet of epithelial cells forming a part of the peduncle of the epiphysis constitute a body which may easily be regarded as an imperfectly developed pineal body. It would be possible to interpret in this way the description given by Stieda of the epiphysis of turtles. He says: "Eine besondere Epiphysiscerebri existirt bei der Schildkröte nicht; das kleine keilförmige Körperchen, welches den dritten Ventrikel und das Zwischenhirn von oben deckend zwischen die hinteren Abschnitte des Lobi hemisphærici eingeschoben ist, zeigt sich bei mikroskopischer Untersuchung nur als Plexus chorioideus des Zwischenhirns oder des dritten Ventrikels. Nervöse Elemente sind nicht zu erkennen." (Ueber den Bau des Centralen Nervensystems der Schildkröte, p. 68.)

The epiphysis of the lizard has already been described. Its general histology is well shown by Fig. 7, Plate III. In longitudinal sections in the horizontal plane the structure has an unmistakable resemblance to that of an undeveloped retina, as seen in the eye of larvæ of amphibians. The pigment clothes the inner wall facing the lumen. Then follows a series of cylindrical cells, whose processes connect with oval cells similar to those of the ganglionic layers of the retina. While it is impossible to trace direct nervous connection with the base, fibres can be followed from the ganglionic layer to the walls of the capsule. There is a lobe of the plexus cephalad and a number of vessels caudad in the sling of connective tissue supporting the organ.

Reference is here made to the valuable paper by Ehlers<sup>(1)</sup>, in which a critical review of previous literature of the epiphysis may be found.

In spite of the great prolongation of the peduncle of the epiphysis in sharks and the cephalad position of the

<sup>1</sup> E. EHLERS, Die Epiphysis der Plagiostomen, Zeitschrift f. Wissensch. Zoologie, xxx, Suppl.

body itself with reference to the brain, the relations to the habena and the surface seem similar to those in the lizard.

The epiphysis in *Petromyzon* is more complicated, but obviously has a similar structure, so far as the epithelium is concerned. (See *Alborn*, Untersuchungen über das Gehirn der Petromyzonten, Zeitsch. f. Wis. Zoologie, xxxix.)

The relations in *Amphibia* are not essentially different, though the organ in adults of *Anura* has suffered much reduction. The evidence for the sensory, and even the optic nature of the organ is conclusive aside from that of palæontology. The embryonic condition of the epiphysis in the serpents is illustrated by Fig. 5, Plate X.

The structure of the thalamus may be conveniently studied in transverse sections beginning cephalad. In the cerebrum, in the region of the præcommissura, the peduncular fibres begin to aggregate near the ventral and median portion, and sensory bundles arrange themselves laterad from them. The latter are accompanied by fusiform cells. The basal region—*i. e.*, homologue of the pyriform lobe—contains a dense mass of cellular elements, consisting largely of small, dark, spidery cells of the olfactory type. On entering the thalamus the peduncles acquire a circular section, and the æsthesodic fibres arch over the bundle medianly. The median nidulus of the thalamus which occupies the sides of the third ventricle arches over them.

In sections somewhat farther caudad the habena is seen perched, as it were, on the summit of the diencephalon, and well circumscribed ventrally from Meynert's nidulus. The definite contours of the peduncles are soon lost as we proceed caudad.

The optic tracts are everywhere separated from the thalamus by the lenticular gelatinous band forming the substantia negra, entad to which is the nidulus, already described, consisting of slender multipolar or pyramidal cells lying transversely and sending processes toward the tract and cephalomedianly (Fig. 3b, Plate XII). The dorsal region of the

thalamus is here filled with fusiform cells (Fig. 3, Plate XII; Fig. 12, Plate IV, and Fig. 1(a), Plate IV).

At the point where the nates begin to appear in the section (Fig. 1, Plate IV), a strong decussation or commissural system appears connecting the right and left peduncular regions. The decussation is a large one, and is separated in its ventral course from the chiasm by dark fibres which I have homologized in the alligator with the ansulate fibres.

The so-called commissure of von Gudden, above described, extends as far caudad as to the front of the infundibulum, which occupies a position beneath the mesencephalon, the thalamus having been caudo-ventrally appressed upon the corpora quadrigemina.

*The ventral region of the thalamus* may next be noticed. The chiasm is very perfect in the snake. The optic fibres being collected in small bundles, each bundle being crossed by a corresponding bundle of the opposite side. Each of the small bundles is enwrapped with a transverse meshwork of connective fibres, thickly set with deeply staining transverse inoblasts, giving to the optic nerve a different appearance from that of any other cranial nerve.

*The nidulus fornicis inferior* consists of two sharply-defined cell-clustres immediately cephalo-ventral of the interpeduncular nidulus, occupying the caudad aspect of the tuber cinereum. The cells are fusiform and transversely placed. The two niduli are separated in the lizard by a considerable interval. While these cell-clusters ought to be unhesitatingly homologized with the mammillary, no ascending tract to the thalamus was seen, and it may be well to use a name not implying any homology.

In the caudal portion of the tuber at the level of the chiasm, in both the black snake and lizard, are two niduli of pyramidal or irregularly multipolar cells, rather larger than those of the surrounding gray matter. They occupy a position some distance laterad from the median line, and are quite distinct from the interpeduncular nidulus, as well



as the nidulus of the fornix. The general direction of the processes seems to be latero-caudad. An exactly similar group of cells appears in the medulla with the ventral longitudinal tracts and these two niduli are more or less united and may be regarded as outlying accessory niduli of that tract, a view which is confirmed by the motor facies of the cells.

In sections at a little higher (dorsad) level than the chiasm the cells are massed in great numbers in the cephalad part of the tuber cinereum, constituting a more or less definite nidulus. The cells are of the fusiform bipolar variety, and lie with their axes dorso-ventrad and fibre-tracts continuing their dorsal projections. This nidulus continues dorsad for some distance, while retaining its relative position about the ventricle.

A conspicuous nidulus lies immediately entad of the zone of opaque gelatinous substance forming the inner boundary of the optic tract (substantia nigra?). The position of this cell group is indicated in Plate II, Fig. 1 a, and Plate I, Fig. 2 a. The general appearance of these cells is illustrated on Plate II, Fig. 12. They are of the so-called motor type, being susceptible to stain and of pyramidal form, while their apical processes extend entirely through the substantia nigra. The cells are narrow and produced, with the long axis in the ento-ectal direction. At right angles to these cells are others of the fusiform type, with clear large nuclei. It seems quite certain that the ental fibres from the above described pyramidal cells pass cephalad, while the peripheral fibre of each seems to fuse with the optic tract. The substantia nigra is itself divided into two portions, causing a similar division of the nidulus, due perhaps to the entrance of large blood-vessels separating a more dorso-caudad portion from that forming the lenticular sheet just entad to the optic tracts.

Of the *cranial nerves* derived from the cephalad part of the brain, only the following jottings on the olfactory

are necessary. In the embryos of the black-snake, frequently referred to above, the fibres from the greatly elongated olfactory lobe collect in rather small bundles and pass to the Schneiderian epithelium either of the nasal cavity or of Jacobson's organ. The fibres destined to the latter collect from the mesal aspects of the lobes and form strong bundles passing ventrad, though there is no sharp regional differentiation. The epithelium of the two organs at this stage is nearly identical, but the granular sub-epithelial layer of the nasal passages is nearly homogeneous, while that of Jacobson's organ has a follicular or lobose structure and receives a larger proportion of nerves.

#### BRAIN OF THE TURTLE (*ASPIDONECTES SPINIFER*).

The brain of the small specimen of *Aspidonectes* figured may serve as a rather generalized type for the *Chelonidæ*. In many respects the external configuration reminds one of that of the lizard. The abrupt flexures described by the axis and the extremely small size of the hemispheres are best seen from sections. The olfactory lobes are superficially fused ventrally and are so closely appressed upon the hemisphere that they may easily be regarded as a part of the latter. The real shape of each of the hemispheres is a very obliquely-placed ellipsoid, bearing a more or less conical protuberance cephalad. The diencephalon presents no noteworthy peculiarity, except the great relative size and independence of the medi-commissura. The optic lobes are very high and large, their median length being much greater than that of cerebrum. The ventricles of the mesencephalon are large and extend far laterad, while the tectum is highly developed.

*Histology.*—In the turtle the distinctions between the areas of pyramidal and fusiform cortical cells are quite obvious. The whole lateral surface is covered by a thin layer of the pyramidal cells with deeply staining nuclei. In the perpendicular section (Fig. 2, Plate III) through the lateral

portion of the hemisphere, the parieto-frontal lobe (a) is made up of these kinesodic cells.

The same lobe in sections further mesad is greatly reduced (Figs. 2 and 3, a), having been encroached upon by a dense mass of the spherical bodies constituting the central granular part of the olfactory lobe. This close approximation of the olfactory lobe upon the hemispheres has the effect of apparently driving the frontal lobe ventrad, for there is a small cluster of pyramidal cells at the point represented at Fig. 4, c. Almost the entire dorsal surface also bears cells of the kinesodic type.

The cells of the occipital lobe, on the other hand, have the spindle shape and large clear nuclei of the typical æsthesodic cells.

The olfactory bulbs are very large and are soldered obliquely upon the front of the cerebrum and ventrally are fused with each other, producing an effect not unlike that seen in *Rana*.

The histological structure is similar to that in the alligator. Externally, especially cephalad and ventrad, is the area of convoluted olfactory fibres, each bundle being separated from its neighbor by sheathing fibres richly filled with dark elongate inoblastic nuclei and scattered oval Deiters' corpuscles. Then follows the glomerary zone of gelatinous aspect, in which almost the only cellular elements resemble Deiters' nuclei. An intervening zone nearly devoid of cells separates this from the cortex olfactorii proper, in which, besides Deiter cells, there are two distinct elements: first, large, irregularly-angular or fusiform cells, with clear granulated nuclei of large size; second, small, densely staining multipolar cells such as we have elsewhere recognized as characteristic of the prosencephalic olfactory regions. This variety of cells is abundant, for example, along the ventral surface of the cerebrum in rodents. The nuclei of these cells are irregular and stain deeply. Separating this zone from the medullary portion is a second layer nearly devoid of



cells. The medullary portion lying near the ventricle contains cells of two sorts, the ordinary Deiter cells, with clear granular nucleus and no obvious cell body, and deeply staining nuclei of smaller size, which perhaps belong to the connective tissue system. There is a small branch of the olfactory (Plate III, Fig. 4, ol. 2) which, after separating from the main portion, passes along the ventral surface of the bulb, without entering it, until it terminates in a detached ventro-caudad portion of the glomerular layer.

The structure of the pyriform lobe is illustrated by Fig. 14, Plate X. The small, irregularly pyramidal or multipolar cells scattered among the fusiform remind one at once of the corresponding region in mammals. The chief difference between these cells and those of the motor type lies in their smaller size, greater irregularity and greater avidity for stains.

The basi-occipital lobe is considerably developed, especially immediately dorsad to the basal part of the ventricle, and projects as a distinct tuber into the posterior cornu (Plate III, Fig. 3, ol.). Dorsad and cephalad to the basi-occipital lobe is a tract forming a curved roof-like partition between it and cephalad parts of the brain. This tract is densely filled with spindle-cells with axes chiefly parallel to the general direction of the tract, descending from the dorso-cephalad angle of the posterior cornu obliquely cephalo-ventrad to the basal part of the ventricle. Thence the tracts and accompanying cells seem to pass caudo-laterad toward the peduncles. A considerable axial portion of the cerebrum lies beneath (ventral to) the anterior cornu, but may be regarded as a part of the central lobe.

All of these axial portions, but especially the occipito-basal, contain rosette-like clusters of fusiform cells. These are obviously due to successive subdivision of cells; in fact, all stages of such subdivision may be found, extending from single cells with double nuclei to rosette-like clusters within clear spaces in the neuroglia. It sometimes appears as

though certain cells suffer subdivision into nucleus-like bodies or Deiters' corpuscles, but of this there is insufficient evidence. In the cephalad part of the axial lobe there is a special mass of proliferating cells. The multiplication here is the same as that in the occipito-basal lobe—longitudinal fission rather than the endogenous multiplication described beyond by Mr. Turner in the corresponding region of birds.

*Miscellaneous Notes.*—The two commissural systems of the habena are well shown, as is the connection with the epiphysis. The latter is constructed obviously upon the same plan as that of the lizard, and, in the present case at least, is of moderately large size. This fact makes it the more surprising that Stieda should have overlooked the existence of a true epiphysis in the turtle. It is true that the body is obscured by the large plexus which envelops it, but a glance at Fig. 7, Plate III, will show that the nervous connection with the habena is complete, and the neuro-epithelium of the tube is also very similar to that of the lizard. The tubular organ is curved cephalad so as to become somewhat sickle-shaped. The peduncle is hollow throughout, and opens not into the third ventricle directly, but into the canal connecting the optic ventricle with the dorsal part of the third ventricle.

The optic ventricle is large and its cornua extend far laterad. The tectum opticum is very thick and has the usual structure, except that in the median portion immediately above the ventricle and lying in the inner zone of concentric cells there is an unusual development of the balloon cells mentioned in the alligator. It is impossible to trace any connection with the trigeminal fibres, however.

In the thalamus the two large niduli, which in the alligator we ventured, for want of a better term, to call corpora geniculata, are in this case very distinct, and lie some distance from the median line beneath the superior commissure (Fig. 5, corp. g.). The niduli themselves consist of large fusiform cells in a homologous stroma of neuroglia. Sur-

rounding these nearly spherical masses is a cortical band of fibrous matter containing densely-packed fusiform cells. This cortical portion of each side is produced mesad to unite with its fellow, thus giving rise to the large medio-commissura (m. c. Fig. 6). These bodies are probably what Stieda refers to when he says: "Ferner schliessen sich die Nervenzellen in den beiden Thalami optici zu einen kugelförmigen Complex zusammen—den Nervenkernel der Thalami."

NOTE.—Attention may be called to the fact, noticed by Stieda, that there is a small ganglion on the root of the eighth (Plate III, Fig. 2), through which the fibres pass mesad to the very large and protuberant eminentia acustica (Plate III, Fig. 4, E, ac.), which projects cephalad, dorsad and mesad into the ventricle below the cephalad part of the cerebellum. This projection it is, no doubt, which Carus<sup>(1)</sup> refers to as "Ganglion des Hörnerven im vierten Ventrikel" which Stieda is unable to identify.

#### PLATE I.

*Figs. 1-4.* Longitudinal horizontal sections of the head of embryo of the guinea-pig at different levels.

*Fig. 1.* Illustrates the relations of the lateral and third ventricles, the formation of the plexus (P), and of the hippocampus (H), as portions of the same fold of cortical substance, and also the existence of two regions (*a* and *b*), where the proliferating cells of the ventricular epithelium come into relation with the cortex, suggesting the possibility of localized deep origin of the mother cells of the cortex in later stages.

*Fig. 2.* Section of the same brain at a more ventral level, the investing structures being removed. The relations of the striatum to the peduncles is well seen.

*Fig. 3.* Similar section from a still lower level, showing results of the strong pons flexure. The medulla and cerebellum are cut transversely, while the paired rudiments of the hypophysis are seen between the Gasser's ganglia. The *recessus lateralis inferior* of the fourth ventricle is nearly closed, and the formation of the lateral niduli of the medulla from the cells of its ventricles is just beginning. The dorsad projection of proliferating cells begins to circumscribe the cerebellum.

*Fig. 4.* A section slightly ventrad to the above, showing especially the dorsad prolongation of the recessus lateralis by which the germinative area of the dorsal surface of the cerebellum is produced. It ultimately becomes soldered upon the cerebellum, forming a double cellular zone.

<sup>1</sup> C. G. CARUS, Darstellung des Nervensystems und Hirns, Leipzig, 1814, p. 172-181.  
L. STIEDA, Ueber den Bau des centralen Nervensystems der Schildkröte, 1875, p. 70.



*Figs. 5-7.* Sections in the same plane from older embryos of the mouse.

*Fig. 5.* Shows the relation of the olives to the roots of the trigeminus, the recessus lateralis inferior being still open in part.

*Fig. 8.* Section near the tip of the cerebellum, showing the double cellular layer of the dorsal surface and also the formation of the plexus and cornucopia.

*Fig. 9.* Portion of the cortex of the cerebellum in an embryo of guinea-pig near the end of embryonic life. The cells of E, the superficial proliferating layer derived from the epithelium of the recessus lateralis, are frequently provided with two or more nuclei. P, zone of Purkinje cells; N, zone of granules containing some large ganglion cells; F, fibre zone with fusiform cells of the nerve sheaths.

*Fig. 10.* Portion of the ventricular region of the same section of the cerebellum with cells of the dentate nidulus. Fig. 4 of Plate II. is a drawing of the entire section.

#### PLATE II.

*Fig. 1.* Portion of the cerebellum and medulla of the mouse embryo figured upon Plate I. and lying dorsad to the section drawn in Fig. 8, showing the two cellular layers, *a* and *c*, and the separating fibres, *b*.

*Fig. 2.* Longitudinal median section of the optic lodes and cerebellum of guinea-pig embryo at an early stage. *V. p.*, velum medullare posterior; *cb.*, cerebellum.

*Fig. 3.* Longitudinal section of the cerebellum of the mouse.

*Fig. 4.* Nearly median longitudinal section of the brain of a guinea-pig embryo near the end of embryonic life, showing the gray proliferating zone on the surface of the cerebellum (an embryonic character) and the proliferating cortex.

*Fig. 5.* Highly magnified cells of the deeper portions of the dorsal cortex. The portion drawn lies nearly one-fifth the whole length of the cerebrum from its caudad margin and nearly in the middle of the width of the hemisphere. The divisions indicated in the scale have the approximate value of 1.25 micros.

#### PLATE III.

Sections from the brain of a young turtle, *Aspionectes spinifer*.

*Figs. 1-6.* Longitudinal sections passing from the lateral to the median plane. *V. g.*, Gasser's ganglion; *G. viii*, ganglion of the eighth nerve; *P*, pes pedunculi; *a*, frontal lobe; *b*, parietal lobe; *c*, fronto-median lobe(?); *o. b. l.*, occipito-basal lobe (part of so-called striatum or axial lobe); *c. p.*, corpus posterius; *v. p.*, velum medullare posterior; *c. c.*, corpus callosum; *a. c.*, præcommissura; *m. c.*, medicommissura; *ep.*, epiphysis; *gl.*, glomerular zone of the olfactory lobe; *cp. g.*, corpus geniculatum.

*Fig. 7.* Epiphysis and habenæ.

*Fig. 8.* Portion of the olfactory cortex, with its three sorts of cells.

*Figs. 9-11.* Views of the brain in three positions.

(All the figures of this plate were drawn with the aid of the camera lucida).

#### PLATE IV.

*Figs. 1-11.* A series of transverse sections through the mesencephalon and metencephalon of the lizard, especially to illustrate the relation of the cerebellum to adjacent parts.

Explanations of these figures will be given in the second part of the paper.

*Fig. 1.* Section just cephalad to the optic lobes. *a*, nidulus of the substantia nigra; the reference line passes through the optic tracts and substantia nigra.

*Fig. 2.* Section through the middle of the optic lobes. *M.b.*, Meynert's bundle.

*Fig. 4.* Illustrates the relations at the base of the cerebellum and exit of the eighth nerve. The free tip of the cerebellum, having recurved to beyond the origin, appears as an independent organ.

*Figs. 5-9.* Indicate the method of retroflexion by which the cerebellum is formed.

*Fig. 12.* Cells from the nidulus of the substantia nigra. See Fig. 1, *a*.

*Fig. 13.* Cells from the root of the tenth nerve, drawn with a one-fifth inch objective.

*Fig. 15.* Cells from the frontal lobe (see Fig. 6, *x*, Plate IX).

*Fig. 16.* Cells from the intra-ventricular lobe of the same section at *x*.

#### PLATE IX.

A series of horizontal sections through the brain of the lizard. The descriptions will be extended in Part II.

*Fig. 1.* Section near the ventral surface. *a*, tuber cinereum.

*Fig. 2.* Section at a higher level. *P*, peduncles; *a*, nidulus of the nigra; *opt.*, optic tracts.

*Fig. 3.* *M.b.*, Meynert's fasciculus; *m.f.*, posterior longitudinal fasciculus.

*Fig. 4.* Section at the level of the corpus callosum.

*Fig. 6.* *F.l.*, frontal lobe; *F.m.l.*, fronto-median lobe; *O.l.*, occipital lobe; *M.L.*, intra-ventricular lobe; *A.P.*, foramen of Munro; *A.L.*, central division of axial lobe; *O.t.*, optic tracts; *O.c.*, posterior or optic-lobe commissure; *M.b.*, Meynert's bundle; *O.v.*, optic ventricle; *H.*, habena; *t.p.tr.*, tract to corpus posterius; *x'* and *x*, see Figs. 15 and 16, Plate IV.

*Figs. 8-9.* *C.p.*, corpus posterius.

## LABORATORY TECHNIQUE.

*A new operating-bench.*—For operating upon the brain of dogs or other animals, especially in cases where anæsthetics cannot be employed throughout, the usual bench is very inconvenient. The following substitute is suggested:

A low bench is provided with two davits, which may be elevated or depressed at will. From these davits are suspended two straps ending in a surcingle, to be strapped about the body of the animal immediately in front of the hind legs and just behind the fore legs respectively. To the posterior surcingle a breech strap is attached, and to the anterior one a breast strap. The two surcingles are connected below with a longitudinal bar, which in use will pass between the legs and extends forward to the head. Anteriorly it supports a halter passing over the neck and nose and a perforated tin or leathern receptacle for the anæsthetic, so arranged as to fit over the nose of the animal. The longitudinal bar may be firmly clamped to a sliding vertical bar at any elevation. The animal is placed on the bench, the surcingles and halter buckled in place, and the davits elevated to the required height. The ventral bar is then firmly clamped, and every motion of the limbs is unimpeded, while, at the same time, the most violent struggles do not produce change of position in the head or trunk. Adduction is absolutely unrestricted, and it is possible at a moment's notice to bring the feet in contact with the bench to observe practical application of the contractions induced, etc.

## MORPHOLOGY OF THE AVIAN BRAIN.

### I.—TAXONOMIC VALUE OF THE AVIAN BRAIN AND THE HISTOLOGY OF THE CEREBRUM.

C. H. TURNER.

*Introduction.*—This communication is the first of a series of papers upon the avian brain. In these papers the author does not think to exhaust the subject. If he succeeds in directing attention to a much-neglected branch of neurology he will consider that his labors have been well repaid.

*Material.*—The remarks in this paper are based upon the study of over one hundred and fifty birds, belonging to nine orders, twenty families, more than forty genera, and above fifty species. In most cases I have had several specimens of the same species; in a few cases, however (*Bubo virginianus*, *Botaurus mugitans*, *Butorides virescens*, *Ardea herodias*), I have had only one specimen. The major part of the bird brains were collected by me during the summer and autumn of 1890. The remainder were donated. For these donated specimens I am indebted to the following gentlemen: to Professor C. L. Herrick, for a specimen of *Ardea herodias* and several other brains; to Professor W. G. Tight, for a specimen of *Botaurus mugitans*; and to Mr. C. J. Herrick, for a specimen of *Bubo virginianus*.

I must confess that I have not read all that has been written upon the avian brain; but, through the kindness of

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<sup>1</sup> Thesis offered for the degree of Bachelor of Science in Biology, Univ. of Cincinnati.



Professor Herrick, I have been enabled to consult the greater part of the recent and a number of the older works upon this subject. In this connection, I thank Prof. Herrick, not only for the use of his library, but also for many valuable suggestions.

*Technique.*—Almost all of the brains examined were hardened in dilute chrom-acetic acid and alcohol. A solution of chrom-acetic acid of from one-third to one-half of the ordinary strength was found to be the most useful. The fresh brain was placed in this fluid and allowed to remain for twelve hours. It was then thoroughly washed with distilled water and hardened in increasing strengths of alcohol. After a specimen had been in 90 per cent. alcohol for a short time, measurements were taken and its external appearance was recorded.

*Staining.*—In preparing specimens for histological study, several stains were tried. In a few cases, Kleinenberg's hæmatoxylin gave good results; in others, it was a failure. Grenacher's hæmatoxylin, applied to sections, sometimes gave good results.

The best results, however, were obtained from aluminium sulphate cochineal.<sup>(1)</sup> In using this stain, the specimens were transferred from 90 per cent. alcohol to 70 per cent. After remaining for one day in this grade of alcohol they were transferred to the stain and allowed to remain in it for three or four days. They were then thoroughly washed in 70 per cent. alcohol, after which they were hardened and sectioned in the usual way.

When the brains are prepared in this manner, the neuroglia does not stain at all, while the nerve cells are stained and their nuclei and nucleoli well differentiated. The red blood-corpscles also stain, but they stain much more densely than the nerve cells. Fibres do not stain, but, in most cases, can be readily traced.

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<sup>1</sup> This stain is prepared by substituting aluminium sulphate for the alum in Czokor's alum cochineal.

## EXTERNAL FORM.

*Size.*—Compared with the brains of other Sauropsida, the bird brain is quite large. It fills the entire cavity of the skull. This cavity is relatively much larger in birds than it is in other members of the same group.

*Compactness.*—The most remarkable characteristic of the avian brain is its compactness. The large prosencephalon entirely covers the diencephalon, and may or may not cover the rhinencephalon and mesencephalon. Along about three-fourths of their mesal border, the two lobes of the prosencephalon are compressed against each other. Near their narrow cephalic end, the two hemispheres are slightly divaricated; near their broad caudal end, they are strongly divaricated<sup>(1)</sup> (Plate V, Figs. 5, 6, 8, 10.)

Into the caudal V thus formed, the cephalic portion of the well-developed epencephalon is wedged so firmly that a portion of it is crowded beneath the prosencephalon. The metencephalon lies beneath the epencephalon, and is almost completely covered by it (Plate V, Figs. 1, 4; Mt.).

*Evolution.*—The compact *encephalon*, the well-developed *epencephalon*, the ventral *mesencephalon*,—all these characteristics completely separate the avian from the reptilian type of brain; yet it is easy to see how the first might have been derived from the second. Allow me to refer to the form of an alligator's brain.<sup>(2)</sup> Viewing the dorsal surface of the brain, we observe the following points. Between the small prosencephalon and the poorly-developed epencephalon, lie the two tangent sub-ellipsoidal lobes of the mesencephalon. In a brain of this type, suppose that the epencephalon de-

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1 A. BUMM transcribes Tiedemann as follows: "The avian brain resembles an ace of hearts, whose apex is directed cephalad and whose base is directed caudad" ("Das Grosshirn der Vögel," von A. Bumm, Zeitschrift für Wissenschaftliche Zoologie, vol. 38, p. 431.

STIEDA makes a similar figure, and then adds: "In die vertiefte Basis des kartenherzförmigen Grosshirn schiebt sich das Cerebellum."

2 See "Notes on the Brain of the Alligator," by Prof. C. L. Herrick, Jour. of the Cincinnati Nat. Hist. Soc., Vol. 12, Pl. VII, Figs. 1, 2, 3.

velops rapidly. As this body grows cephalad and dorsad it will separate the optic lobes. Now let the cerebral hemispheres increase in length. Let the lateral and dorsal portions of each hemisphere grow caudad much more rapidly than the mesal and the ventral. This will cause the caudad portion of each hemisphere to revolve toward the meson, and, at the same time, to over-ride the optic lobe. A comparison of the different lobes found in the avian brain with the corresponding lobes of the reptilian encephalon shows that this mesal revolution has actually been performed.

#### RHINENCEPHALON.

*Size.*—Compared with that of other Sauropsida, the avian rhinencephalon is quite small. In most birds, its length is equal to about 10 per cent. of the length of the brain; but in some types (*Ardeidae*, *Anatidae*), this ratio rises to 18 or 20 per cent.; while in others (*Corvidae*), it falls to about 6 per cent.<sup>(1)</sup> (see Table I).

*Form.*—With regard to position, the avian rhinencephala fall into two classes. Into the first class fall those which project beyond the cephalic end of the prosencephalon; into the second class fall those which do not thus project.<sup>(2)</sup>

Each rhinencephalon of the first class consists of two elongated sub-ellipsoidal bodies which arise side by side, either at or immediately ventrad to the cephalic end of the prosencephalon, and project cephalad. Each of these lobes contains a ventricle, which, I think, is always continuous with the lateral ventricle of the cerebral hemisphere.

Each rhinencephalon of the second class consists of one or two short sub-ellipsoidal bodies which are partly imbedded

<sup>1</sup> After carefully studying the cerebrum of European birds, A. Bumm remarks: "In swimming birds, the olfactory lobes are well developed; in wading birds (*Sumpfvögel*), they are moderately developed; in all other cases, they are only slightly developed." He then adds the following table:

*Ratio of the weight of the Rhinencephalon to the weight of the Prosencephalon.*—In the goose as 1:67.0; in the snipe as 1:84.5; in the buzzard as 1:543.0. Op. cit., p. 436.

<sup>2</sup> In European birds, these two types of rhinencephalic structure have been recognized by A. Bumm. Op. cit., p. 435.

in the prosencephalon. When there is only one lobe, it is the result of the fusion of the primitive lobes. When two lobes are present, each usually contains a ventricle; but when there is only one lobe, it is usually solid.

The above types merge into each other. As we ascend the scale, the olfactory lobes move caudad and become smaller. In the higher groups, the lobes are fused and almost completely imbedded in the prosencephalon.

#### EXPLANATION OF TABLE I (SEE P. 78).

"Length" is a contraction for "Ratio of the length of the rhinencephalon to the length of the brain."

"Breadth" is a contraction for "Ratio of the breadth of the rhinencephalon to the length of the brain."

All ratios are expressed in hundredths of the length of the brain.

"Partly imbedded" is a contraction for "Partly imbedded in the prosencephalon."

A + affirms what is at the head of the column.

A — denies what is at the head of the column.

#### PROSENCEPHALON.

*Size.*—In carinate birds, the prosencephalon is relatively very large. In the birds examined, the dimensions vary in different groups; thus, the ratio of the length of the prosencephalon to the length of the brain varies from about 55 per cent., in the *Ardeidae*, to about 92 per cent., in the *Corvidæ*; the ratio of the breadth of the prosencephalon to the length of the brain varies from about 80 per cent., in the *Ardeidae*, to about 125 per cent., in the *Corvidæ*; the ratio of the depth of the prosencephalon to the length of the brain varies from about 45 per cent., in the *Ardeidae*, to about 68 per cent., in the *Corvidæ*<sup>(1)</sup> (see Table II).

In all types, the depth of the prosencephalon is less than its length. In the *Anatidæ*, the length and breadth are about

<sup>1</sup> After having carefully weighed the brains of various European birds, A. Bumm compiled the following table:

*Ratio of the Weight of the prosencephalon to the weight of the remainder of the brain.*

—In the oscinine birds, 2.79 : 1; in the fringilline birds, 2.77 : 1; in the parrots, 2.08 : 1; in the swimming birds, 1.94 : 1; in the wading birds (Sumpfvögel), 1.75 : 1; in the birds of prey, 1.61 : 1; in the fowls, 1.12 : 1; in the doves, 0.95 : 1. Op. cit., p. 433.



equal. In all other cases, the breadth exceeds the length<sup>(1)</sup> (see Table II).

#### HEMISPHERES.

As usual, the prosencephalon is composed of two hemispheres, which are compressed against each other at the meson. Each hemisphere is a gibbous sub-conical body, with its apex directed cephalad and its base directed caudad. The ventral surface of each hemisphere is undulating; the lateral surface may be either longitudinally undulating or convex; the mesal surface is flattened; the cephalic, dorsal and caudal surfaces are convex.

*Connections.*—At the meson, the hemispheres are separated by a deep longitudinal fissure (*Fissura longitudinalis*). The hemispheres are connected with each other by the anterior commissure and the corpus callosum. The hemispheres are connected with the diencephalon by the crura cerebri.

*Dorsal aspect* (Plate V, Figs. 5, 6, 8, 10).—Viewed from above, the outline of each hemisphere of the avian brain is composed of the following elements:

1. A short convex curve, which passes caudo-mesad from the cephalic extremity of the hemisphere to the meson.
2. A straight line, which continues this curve caudad along almost the entire mesal border.

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<sup>1</sup> The following tables show that there is a great resemblance between the brains of American and of European birds. All these tables are translated from A. Bumm's work on the avian prosencephalon. Op. cit., p. 431-432.

*Table of ratios of the transverse to the longitudinal diameter of the avian prosencephalon* (compiled by Leuret, after an examination of thirty-six species).—In the parrots, 1 : 1.09; in the swimming birds, 1 : 0.99; in the fringilline birds, 1 : 0.91; in the oscinine birds, 1 : 0.81; in the wading birds, 1 : 0.79; in the fowls, 1 : 0.79; in the birds of prey, 1 : 0.74; in the doves, 1 : 0.74.

*Table of ratios of the width to the length of the avian prosencephalon* (compiled by Serres, after the examination of thirty-one species).—In the parrots, 1 : 1.00; in the oscinine birds, 1 : 0.85; in the wading birds, 1 : 0.85; in the swimming birds, 1 : 0.80; in the running birds, 1 : 0.76; in the birds of prey, 1 : 0.70; in the fowls, 1 : 0.66.

*Table of ratios of the length to the depth of the avian prosencephalon* (compiled by Serres).—In the fowls, 1 : 0.75; in the running birds, 1 : 0.69; in the birds of prey, 1 : 0.69; in the swimming birds, 1 : 0.60; in the wading birds, 1 : 0.60; in the parrots, 1 : 0.59; in the oscinine birds, 1 : 0.58.

3. A convex curve, which extends caudo-laterad from the caudad extremity of the second curve to the caudad extremity of the hemisphere.

4. A convex curve, which extends cephalo-laterad from the caudad extremity of the third curve to the widest part of the prosencephalon, then cephalo-mesad to the cephalic extremity of the same. The widest part of the prosencephalon is nearer its caudad than its cephalad extremity.

This is the usual appearance; but, in some types (*Ardeidæ*, *Cuculidæ*, *Meleagrididæ*, *Domestic Fowl*, *Turdidæ*), the caudad and cephalad portions of the fourth curve are convex, while the middle portion is concave (Plate V, Figs. 6, 8). Each of the above curves grades so smoothly into its successor that it is impossible to say where one curve ends and another begins.

When the two hemispheres are in their natural position, their combined outlines form a V at each extremity of the prosencephalon. The smaller, cephalic V, is formed by the intersection of curve number one of one hemisphere with the corresponding curve of the other hemisphere. The larger, caudal V, is formed by the intersection of curve number three of one hemisphere with the corresponding curve of the other hemisphere.

In the *Anatidæ* (Plate V, Fig. 5) and *Ardeidæ* (Plate V, Fig. 6) the caudal V is very shallow. As we ascend the scale, this V becomes deeper and deeper (Plate V, Figs. 8, 10). This I consider an affirmation of the above theory; that, in its evolution, the lateral border of each hemisphere extends caudad much more rapidly than the mesal. This causes the caudal border of each hemisphere to revolve towards the meson. The depth of the caudal V is a function of this revolution, and varies directly as the amount of revolution. According to this theory, the caudal V should be shallow in the lower and deep in the higher types of avian brains. Since this is the cases, I think we have an important confirmation of the truth of the theory.

*Lateral view* (Plate V, Figs. 1, 4).—Viewed from the side, the outline of the avian prosencephalon is composed of the following curves:

1. A convex curve, which extends caudo-dorsad from the cephalad to the dorsad extremity of the prosencephalon, where it turns and passes caudo-ventrad to the caudad extremity of the prosencephalon. Here the curve turns again, and, for a short distance, passes cephalo-ventrad.

2. A broken line, composed of two or three convex curves, which extends cephalad from the end of the above curve to the cephalad extremity of the prosencephalon.

In the lower types of avian brains, the cephalad portion of curve number one slopes more gradually towards the base of the brain than it does in the higher types.<sup>(1)</sup>

*Dorsal fissure*.—This fissure is universally present, but is not always in the same position (Plate V, Figs. 1, 4, 5, 6, 7, 8, 10; DF).

In the *Anatidae* (Plate V, Fig. 5, DF), this is a convex curve, which lies upon the dorsal surface of the prosencephalon. It arises from the meson at about one-third of the length of the cerebrum from the cephalad extremity of the brain. For more than half of its course, this curve passes caudo-laterad; then it passes caudo-mesad to the caudad extremity of the cerebral hemisphere, where it merges into that border of the hemisphere. The greatest width of this curve is equal to about one-half of the greatest width of the cerebral hemisphere.

In the *Icteridae* (Plate V, Fig. 7, DF), this curve is also convex; but it has its origin upon the ventral surface of the brain. Slightly caudad to the rhinencephalon, it arises from the meson and extends cephalo-laterad for a short distance, then it passes caudo-dorsad to the dorsal surface of the prosencephalon.

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<sup>1</sup> According to A. Bumm, this is also true of the brains of European birds. *Op. cit.*, p. 438-439.

At first sight these two fissures appear to be distinct, but I have considered them identical:

1. Because Bumm has done so.<sup>(1)</sup>
2. Because both are never found in the same species.
3. Because I find all the intermediate stages.

In the *Anatidæ* (Plate V, Fig. 10, DF) this fissure lies entirely upon the dorsal surface of the brain and is very long.

In the *Picidæ* (Plate V, Fig. 10, DF) it lies upon the dorsal surface of the prosencephalon, but it is near the cephalic extremity of the same. It is also very short. In the *Cuculidæ*, *Ardeidæ*, *Meleagrididæ* and *Strigidæ* this fissure arises from the ventral surface of the brain, between the origin of the rhinencephalon and the cephalad extremity of the prosencephalon and terminates upon the dorsal surface of the cerebral hemisphere (Plate V, Figs. 1, 4, 6, 8; DF).

In the *Icteridæ* (Plate V, Fig. 7) it arises from the ventral surface of the prosencephalon caudad to the rhinencephalon and terminates upon the dorsal surface of the cerebral hemisphere.

*Dorsal tuber.*—The dorsal fissure either partly or entirely surrounds a slight swelling. This swelling I have called the "dorsal tuber." Since the dorsal fissure surrounds the dorsal tuber, whenever a portion of that fissure is on the ventral surface of the brain, a portion of the dorsal tuber is also carried ventrad.

On the ventral surface are several tubers. These may be studied to the best advantage in the owl brain (*Bubo virginianus*), where they are enormously developed (Plate V, Fig. 1).

*Ventro-frontal tuber* (Plate V, Figs. 1, 13).—This is a small swelling which is situated upon the ventral surface of the prosencephalon at the meson and near the cephalad extremity of the hemispheres. When this tuber is present, the rhinencephalon is situated immediately ventrad to it.

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<sup>1</sup> Op. cit.; Taf. 24; Figs. 1, 5; WFL.



This tuber is usually absent. In such cases the dorsal tuber may be mistaken for it.

*Ventro-median tuber* (Plate V, Figs. 1, 7, 9, 13).—This is a convex swelling, the sides of which slope gently in all directions. It lies upon the mesal half of the prosencephalon between the rhinencephalon and the optic chiasm. In some species (Plate V, Figs. 1, 9, 13) this tuber is quite large, in others (Plate V, Fig. 7) it is small, in still others it is apparently absent.

*Ventro-lateral tuber* (Plate V, Figs. 1, 4, 7, 9, 13).—This tuber is almost universally present. It is usually the largest tuber of the brain and seems to be the homologue of the pyriform tuber of mammals. It is a relatively large swelling, which is situated at the caudo-lateral angle of the ventral surface of the cerebral hemisphere. Laterad, caudad, and mesad, the surface of this tuber is strongly convex; cephalad, the surface is slightly convex. This surface of the tuber slopes gradually towards the surface of the prosencephalon. Its length is usually a little more than one-third that of the prosencephalon while its breadth is usually a little more than half the breadth of the hemisphere.

*Innominate tuber*.—This is a small, slightly developed tuber, which I have occasionally noticed. It is situated somewhat mesad to the ventro-lateral tuber and is partly covered by the optic lobe. Its small size and the irregularity of its presence cast some doubt upon the propriety of recognizing it as a distinct tuber.

#### EXPLANATION OF TABLE II (SEE P. 80).

"Length" is a contraction for "Ratio of the length of the *prosencephalon* to the length of the brain."

"Breadth" is a contraction for "Ratio of the greatest breadth of the *prosencephalon* to the length of the brain."

"Depth" is a contraction for "Ratio of the greatest depth of the *prosencephalon* to the length of the brain."

All ratios are expressed in hundredths of the length of the brain.

The length of the brain is the distance from the cephalic extremity

of the *prosencephalon* to the center of the diamond-shaped depression that lies immediately caudad to the twelfth nerve root.

Dorsal fissure median is a contraction for intersection of the dorsal fissure with the meson visible from above.

Dorsal fissure frontal is a contraction for intersection of the dorsal fissure with the meson not visible from above.

A + affirms the presence of the fissure or tuber mentioned at the top of the column.

A — denies the presence of the fissure or tuber mentioned at the top of the column.

#### MESENCEPHALON.

The avian mesencephalon consists of two subellipsoidal bodies, which lie partially or wholly beneath the prosencephalon. Each lies in a special cavity of the skull. These lobes have no visible connection either with each other or with the diencephalon. They are usually smooth, but occasionally there is a faint indication of a transverse fissure.

*Size.*—In the same family the ratios of the dimensions of the optic lobes to the length of the brain are approximately constant. In different families these ratios vary. The ratio of the axial length of the optic lobes to the length of the brain varies from a little less than thirty per cent. in the *Tyrannidae* to a little more than forty per cent. in the *Corvidae* and *Paridae*. The ratio of the greatest breadth of the optic lobes to the length of the brain varies from about twenty per cent. to a little more than thirty per cent. (see Table III).

*Types.*—With regard to position, the avian mesencephala fall into two classes. Those in the first class are entirely covered by the prosencephalon, while those in the second are only partially covered.

When belonging to the second class the caudal portion of each optic lobe lies immediately laterad to the epencephalon and immediately caudad to the prosencephalon. Thence it extends ventro-cephalo-mesad to beneath the prosencephalon.

When belonging to the first class, each lobe lies immediately ventrad to the diencephalon and has its major axis inclined towards the meson. As in the second class, its caudal end is further from the meson than its cephalic end.<sup>(1)</sup>

Excepting the *Anatidae* and other birds of that type, as we ascend the scale, the optic lobes become more and more covered by the prosencephalon until in the highest groups there is quite a margin between the caudad extremity of the prosencephalon and the caudad extremity of the optic lobe. (Plate V, Figs. 9, 8, 6, 13, 7.)

This is a natural outcome of the process of cerebral revolution, mentioned above.

#### EXPLANATION OF TABLE III (SEE P. 82).

"Length" is a contraction for "Ratio of the axial length of the optic lobes to the length of the brain."

"Breadth" is a contraction for "Ratio of the greatest width of the optic lobe to the length of the brain."

The length of the brain is the distance from the cephalic extremity of the *prosencephalon* to the center of the rhombic depression immediately caudad to the twelfth nerve root.

+ is a contraction for "Optic lobes entirely covered by the *prosencephalon*."

— is a contraction for "Optic lobes not entirely covered by the *prosencephalon*."

#### DIENCEPHALON..

This portion of the brain is, relatively, small, and is entirely covered by the prosencephalon. A ventral view reveals it as a small sub-rectangular body lying between the prosencephalon and metencephalon. It is intimately connected to the mesencephalon and to the metencephalon, and is also connected, by the *crura cerebri*, to the prosencephalon.

#### EPENCEPHALON.

*Form*.—As stated above, the epencephalon is well developed. Its form is that of a laterally compressed hepta-

<sup>1</sup> Prof. Coues says, that the optic lobes are never covered; this is evidently an oversight. "Coues' Key to North American Birds, 2nd edition, (1884) p. 176."

hedron, with two plane and five convex surfaces. Two faces are formed by the, practically plane, sub-parallel, sides. A third face extends cephalo-dorsad from the caudad extremity of the epencephalon to the dorsal extremity of the same. A fourth face extends cephalo-ventrad from this place to the pineal body. From this place, a fifth face extends, almost perpendicularly, cephalo-ventrad to about where the metencephalon joins the diencephalon. Thence a sixth face extends ventro-caudad to the ventral extremity of the epencephalon. The solid is closed by the seventh face, which extends caudo-dorsad from this place to the caudal extremity of the epencephalon. The last five faces are ectally convex and crenated. In most cases, faces three to seven are of about the same size (Plate VII, Fig. 3).

*Convolution.*—The epencephalon is indented by several transverse fissures, which extend entad from the periphery almost to the ventricle. Near the surface, these fissures are usually increased by the intercalation of one or more fissures between each of the above. Corresponding to each of these fissures, there is a transverse convolution. It is the presence of these convolutions which gives the above-mentioned faces a crenated appearance (Plate VII, Fig. 3).

*Flocculi.*—These are two flaps, one of which projects from each of the lateral surfaces of the epencephalon. They are situated at a short distance caudad to the optic lobes and immediately cephalad to the metencephalon. In the *Anatidae* and *Ardeidae* (Plate V, Figs. 4, 5, 6, 9), these flaps are sub-triangular; in the *Passeres*, *Picariae*, *Strigidae*, etc. (Plate V, Figs. 1, 7, 8, 10), these flaps are sub-rectangular. Each flocculus is almost completely imbedded in a special cavity of the skull.

*Ventricle.*—In the center of the epencephalon there is a small ventricle, which is connected to the fourth ventricle by a narrow neck.

*Proportions.*—In the *Anatidae* (Plate V, Fig. 5), the epencephalon is wider than long; in all the other families



that I have studied, it is longer than wide (Pate V, Fig. 6).

*Connections.* — The epencephalon is connected to the metencephalon by the *crura cerebelli*.

#### EXPLANATION OF TABLE IV (SEE P. 84).

"Length" is a contraction for "Ratio of the length of the *epencephalon* to the length of the brain."

"Breadth" is a contraction for "Ratio of the greatest width of the *epencephalon* to the length of the brain."

"Depth" is a contraction for "Ratio of the depth of the *epencephalon* to the length of the brain."

"The length of the brain is the distance between the cephalic portion of the prosencephalon and the centre of the rhombic depression that lies immediately caudad to the twelfth nerve root."

The length of epencephalon used is the distance between the apex of the caudal V of the prosencephalon and the caudad extremity of the epencephalon.

All ratios are expressed in hundredths of the length of the brain.

#### METENCEPHALON.

The metencephalon lies beneath the epencephalon and is connected with it by the *crura cerebelli*. The metencephalon is intimately connected with the diencephalon.

*Form.*—In form the metencephalon is a sub-rectangular prism, all of the exposed faces of which are feebly convex. Near the caudal extremity of the metencephalon, its lateral and ventral faces slope, abruptly, ento-caudad, to the myelon. On the ventral surface, at the union of the metencephalon and myelon, there is a small diamond-shaped depression (Plate V, Figs. 7, 13).

*Surface.*—The entire surface of the metencephalon is quite smooth. There is no external indications of either pons or pyramids. On the ventral surface, however, there is usually a faint indication of a mesal fissure (Plate V, Figs. 7, 13).

*Proportions.*—The metencephalon is usually from one-half to three-fourths as deep as wide, and about as wide as long (see Table V).

*Fourth ventricle.*—As usual, the metencephalon contains

the fourth ventricle, which is entirely covered by the ependymal layer.

#### EXPLANATION OF TABLE V (SEE P. 86).

"Length" is a contraction for "Ratio of the length of the *metencephalon* to the length of the brain."

"Breadth" is a contraction for "Ratio of the greatest breadth of the *metencephalon* to the length of the brain."

"Depth" is a contraction for "Ratio of the greatest depth of the *metencephalon* to the length of the brain."

All ratios are expressed in hundredths of the length of the brain.

The length of the brain is the distance between the cephalic extremity of the prosencephalon and the center of the rhombic depression which lies immediately caudad to the twelfth nerve root.

*Pineal body*.—This is always present (Plate V, Figs. 5, 6, 8, 10). It is a small sub-conical body, which lies in the caudal V of the prosencephalon. The apex of this cone points ventrad. From it the habenula passes ventrad, around the cephalic portion of the ependymal layer, to the habenula. The pineal gland is intimately connected with the dura and is liable to be removed with it.

*Infundibulum* (Plate V, Figs. 9, 13).—On the ventral surface of the brain, between the diencephalon and the metencephalon, lies the tuber cinereum, which is pierced by the infundibulum.

*Pituitary body*.—Immediately ventrad to the infundibulum, lies the pituitary body. It is encased in a special cavity of the skull.

#### NERVES.

The external course of the nerves has been so well described by Prof. Elliott Coues<sup>(1)</sup> that it is not necessary for

1. The cranial nerves are twelve pairs, as in mammals, the highest vertebrate number.

1. The *olfactory*, nerve of special sense (smell); origin from rhinencephalon; exit from cranial cavity by olfactory foramen, high up in the orbital cavity; conducted along a groove to find escape between the perpendicular and lateral plates of the ethmoid into the nasal chambers; distributed to the investing mucous membrane of the septal and turbinal bones of the nose. The exit is through a sieve-like or *cribiform* plate only in *Apteryx* and *Dinornis* (Owen).

2. The *optic*, nerve of special sense (sight); origin from optic lobe and thalamus(?); of great size and forming a *chiasm* (decussation) with its fellow; exit by optic foramen, a large hole in the back of the orbital cavity between the centers of orbito-sphenoid and

me to do more than mention the position of the external roots.

*First, or olfactory nerve.*—This nerve arises from the cephalic extremity of the rhinencephalon.

*Second, or optic nerve* (Plate V, Figs. 4, 7, 9, 13).—The optic-fibres arise from the cephalic end of the optic lobe and pass, in a large bundle, to the chiasm. Here they decussate with corresponding fibres of the opposite side, and, after

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ali-sphenoid, close to, or in common with, its fellow. This nerve forms the retina of the eye.

3, 4, 6. The *oculi-motor, pathetic, abducent*, collectively the motor nerves of the eye, supplying the muscles moving the eyeball; 3, to all these muscles, excepting the superior oblique and the external rectus; origin from crura cerebri, base of mesencephalon; 4, to the superior oblique; origin behind the optic lobes, upper surface of metencephalon; 6, to the external rectus (also to the muscle of the third eyelid in birds); 3, 4, 6, exit from the cranial cavity into the orbital cavity by several small, not constant, foramina near the optic foramen; or by this foramen sometimes all of the nerves which enter the orbit pass out of the brain cavity through one great hole.

5. Great *trifacial* or trigeminal, sensori-motor; feeling, skin of head, moving muscles of jaws; origin (double) from myelencephalon, leaves brain from sides of metencephalon; sensory root has gasserian ganglion, motor root simple. This root has three divisions, whence its name: 5 *a*, *ophthalmic* division, the most distinct; exit from cranial into the orbital cavity above and to the outer side of the optic foramen; grooves orbital wall in passing; *ciliary* ganglion; distribution mainly to lachrymal and nasal parts; traceable to end of upper mandible; 5 *b*, *superior maxillary*; exit by foramen ovale, in ali-sphenoid or between that and the prootic centre; distribution to side of upper jaw; *mecklian* ganglion; 5 *c*, *inferior maxillary*, derived chiefly from motor root; exit same as 5 *b*; distribution to lower jaw (muscles, substance of bone, integument); no *special* sense (gustatory function); no *otic* ganglion.

7. *Facial* or *portio dura*, motor. origin from myelencephalon; enters periotic bone, escapes from ear behind quadrate bone, by what corresponds to stylo-mastoid foramen of mammals; communicates with 5 *c* by chordo tympanic nerve, with 9, 10, 12 and sympathetic system; distribution to skin muscles and others of lower jaw and tongue, etc.

8. *Auditory* or *portio mollis*, nerve of special sense (hearing); origin with 7; no exit from skull; enters meatus auditorius internus of periotic bone; forms auditory apparatus in labyrinth of ear.

9. *Glosso-pharyngeal*, mixed nerve, sensori motor and gustatory (taste); origin myelencephalon; exit by foramen in exoccipital bone, behind basi-temporal, near lower border of tympanic recess; distribution to muscles and membranes of gullet, throat, tongue, etc.

10. *Pneumogastric*, sensori-motor; origin and exit next to 9; distribution to wind-pipe, lungs, gullet, stomach, heart, etc.; has recurrent laryngeal to vocal organs.

11. The *spinal accessory*, sensori-motor; origin upper part of spinal cord; exit 9, 10; distribution to these nerves and to muscles of the neck.

9, 10, 11 are intimately connected with one another, and with other nerves, especially 10 with the sympathetic. The several foramina in a bird's skull, which may be seen in the place indicated at 8 (Figs. 69, 70), are for the divisions of this composite *vagus* or "wandering" nerve of respiration, circulation, digestion, etc.; they represent morphologically a *foramen lacerum posterius* between exoccipitals and opisthotic centres.

12. *Hypoglossal*, motor nerve of the tongue; origin from myelencephalon; exit by anterior condyloid foramen in front of occipital condyle.

Thus the plan of the cranial nerves of birds is nearly coincident with that of mammals.—PROF. ELLIOTT COUES, op. cit., pp. 176-7.

emerging, become the optic nerve. This is a very large nerve.

*Third, or oculo-motor* (Plate V, Figs. 9, 13).—This is a small nerve. It arises from the diencephalon near to and laterad to the infundibulum and immediately cephalad to the metencephalon.

*Fourth, or pathetic* (Plate V, Figs. 9, 13).—This is a small nerve. At a short distance caudad of the cephalic extremity of the metencephalon, the fourth nerve emerges from between the mesencephalon and the metencephalon.

*Fifth, or trigeminal* (Plate V, Figs. 4, 7, 9, 13).—This is a large nerve. It arises from the side of the metencephalon, about half way between its dorsal and ventral surfaces and a short distance caudad to the optic lobes.

*Sixth, or abducens* (Plate V, Figs. 7, 9, 13).—At a short distance caudad to the trigeminal nerve and about half way between the meson and the lateral border, the small sixth nerve leaves the metencephalon.

*Seventh and eighth, or facial and auditory* (Plate V, Figs. 9, 13).—A short distance caudad to the trigeminal nerve and near the dorsal surface of the metencephalon, there is a large nerve root. This is the common root of the seventh and eighth nerves.

*Ninth and tenth, or glossopharyngeal and pneumogastric* (Plate V, Figs. 1, 4, 9, 13).—Caudad and slightly ventrad to the seventh and eighth nerve root, the medium-sized root of the ninth and tenth nerves arises from the metencephalon.

*Eleventh, or spinal accessory* (Plate V, Fig. 4).—The eleventh nerve arises, as a number of small strands, from the lateral surface of the metencephalon. Cephalad, this nerve unites with the common root of the ninth and tenth nerves; caudad, it passes beyond the root of the first cervical nerve.

*Twelfth, or hypoglossal*.—This is a small nerve, which arises from the metencephalon at about the same distance from the meson as the sixth nerve and immediately cephalad to the caudal extremity of the metencephalon.



## II.—RELATION OF BRAIN MEASUREMENTS TO TAXONOMY.

Remembering that, owing to its position, the brain would be very little influenced by external agencies, it is thought that the comparative development of the brain should form an important element in the classification of birds. With this idea in mind, Table VI. has been compiled. This table has been arranged, not to give a final classification for American birds, but to illustrate the taxonomic value of the avian brain.

### EXPLANATION OF TABLE VI (SEE P. 88).

The column headed "PROS." contains a classification based upon the relative development of the different parts of the avian brain.

The column headed "HUXLEY" contains Prof. Thomas Huxley's classification. His classification is based upon osteological characteristics.<sup>(1)</sup>

The column headed "PARKER" contains Prof. W. K. Parker's modification of Prof. Huxley's classification.<sup>(2)</sup>

In all cases, excepting that of the *Laridae* and *Colymbidae*, the tabulation is based upon original observation. My notes upon these two groups are based upon a study of sketches by Brännlich<sup>(3)</sup> and by Gmelin.<sup>(4)</sup>

Taking it for granted that a well-developed prosencephalon indicates a high degree of specialization, the majority of the distinctions are based upon the development of that portion of the brain. To say that the olfactory lobes are covered is equivalent to saying that the prosencephalon is flexed. To say that the optic lobes are covered is equivalent to saying that the longitudinal axis of the prosencephalon is quite long.

<sup>1</sup> "On the Classification of Birds: and on the Taxonomic Value of the Modifications of Certain of the Cranial Bones." By Thomas Huxley, F.R.S., V.P.Z.S. Proc. of the Zool. Soc., 1867, pp. 415-472.

<sup>2</sup> Encyclopædia Britannica, ninth edition, Vol. III, p. 605.

<sup>3</sup> United States Geological Survey, J. W. Powell, Director: third annual report, 1881-82, p. 56, Fig. 8.

<sup>4</sup> Ditto, p. 70, Fig. 20.

After examining a large number of bird brains, it was decided to divide the carinate birds into two major groups. In the first group, which has been called "A," the greatest width of the prosencephalon is more than 90 per cent. of the length of the brain. In the second group, which has been called "B," the greatest width of the prosencephalon is less than 90 per cent. of the length of the brain. The waders and fowls and their affines are placed in group "A." The remainder of the carinate birds fall in group "B."

From the first appearance of the class Aves until now, there has been a gradual retrograde evolution of the avian rhinencephalon. In the lowest types, the rhinencephalon is terminal and is composed of two distinct lobes; in the highest types, the rhinencephalon is not only not terminal, but it is covered by the prosencephalon and partly imbedded in it. In these types, the two lobes of the primitive rhinencephalon have fused to form a small single lobe.

In the light of these facts, group "A" has been subdivided into two minor groups, "a" and "b." In those brains that fall into group "a," the partly imbedded rhinencephalon is entirely covered by the prosencephalon and is composed of a single lobe. In those brains that fall into group "b," the partly imbedded rhinencephalon is covered, but it is composed of two lobes.

Upon the same principle, group "B" has been subdivided into two minor groups, "c" and "d." In those brains that fall into group "c," the rhinencephalon is composed of two lobes and is sub-terminal. In those brains that fall into group "b," the rhinencephalon is composed of two lobes and is terminal.

These minor groups have been redivided into two groups. In this case the position of the optic lobes has been the criterion. Division "I" includes those birds in which the optic lobes are entirely covered by the prosencephalon; division "II" contains those in which the optic lobes are only partially covered.

As in all natural schemes of classification, these minor groups overlap each other. To determine the position of doubtful cases, other characteristics have been tabulated.

To determine the position of a family within the smallest subdivision, the relative size of the prosencephalon has been considered a convenient criterion.

A series of either gravimetric, volumetric or linear measurements would have furnished the desired data. Not being able to use all three, it was necessary to decide which of these three would best serve our purpose. Both volumetric and gravimetric measurements possess some advantages, but the errors introduced by attempting to separate the various parts of a small brain are so great that all the advantages of the measurements are negated.<sup>(1)</sup>

There is also an objection to linear measurements. During the process of hardening some brains are slightly flattened. In one brain this flattening will lengthen one diameter, while in another brain it may shorten it. It is evident then that ratios based upon any one diameter of the prosencephalon would not serve our purpose. It is also certain that any pressure which causes an increase or decrease in the length of one diameter will also cause a compensating decrease or increase in some other diameter. Hence, if the ratios of the relative lengths of three diameters at right angles to each can be conveniently combined, there will result a ratio which will be practically free from errors of manipulation. There are several means by which this combination could be effected. I have used what I consider the most convenient combination. I have multiplied the respective ratios of the length, breadth and depth of the prosencephalon to the length of the brain together and extracted the cube root of the product. The resultant ratio represents

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<sup>1</sup> After attempting to tabulate the relative weights of the olfactory lobes of various birds, A. Bumm remarks: "Abgesehen davon, dass die Abtrennung der Riechhöcker vom übrigen Grosshirn bei den kleinen Vögel nur schwierig and unsicher gelingt, war auch die von mir benutzte Wage für die hier in Betracht kommenden minimalen Gewichts-differenzen nicht empfindlich genug." *Op. cit.* p. 436.

approximately the ratio of the cube root of the volume of the prosencephalon to the length of the brain. This ratio is tabulated in Table II, Column  $\sqrt[3]{(L \times B \times D)}$ . In practice this ratio has proved very convenient. With one exception (*Ardeidae*) the members of the same family differ from each other by less than three per cent.

Upon consulting Table VI, it will be seen that the grouping of the families examined agrees very well with the classification proposed by Prof. Huxley in 1867. Prof. Huxley's classification was based upon osteological characteristics. The fact that this agreement exists is to my mind an excellent testimonial of the taxonomic value of the avian brain.

EXPLANATION OF TABLE VII (SEE PAGE 90).

This table has been constructed to illustrate the value of the  $\sqrt[3]{(L \times B \times D)}$  as a criterion for determining the rank of a family within a group. The passerine group has been chosen because it has been more thoroughly studied than any other group.

In the column headed "Coues" is tabulated the order found in Coues' Key to North American Birds.

In the column headed "A. O. U." is tabulated the order found in the A. O. U. Check List of North American Birds.

In the column headed "Shufeldt" is tabulated the order found in North American Passeres, by R. W. Shufeldt, M.P., C.M.Z.S.

In the column headed  $\sqrt[3]{(L \times B \times D)}$  is tabulated the order suggested by the  $\sqrt[3]{(L \times B \times D)}$ .

It may not be out of place to say a word or two in defense of the arrangement suggested by the  $\sqrt[3]{(L \times B \times D)}$ .

The Corvidæ are placed at the top of the list. This agrees with the arrangement proposed by R. W. Shufeldt. In defending his position, Mr. Shufeldt remarks: "Corvus corax has a skeleton of the highest type of oscine organization, a statement that applies with equal force to much else in the economy; its brain is relatively larger in proportion to the size of the bird than others of the same order; its young substantially have the plumage of the parents at a time when, as nestlings, they first take on their plumage; finally the raven is a far more intelligent bird than any species of Sialia



that the author has ever made psychological study of, and, indeed, than any other thrush. The power of song is by no means an index of a high order of intelligence, much less an indication of a highly specialized organization."<sup>(1)</sup>

The position of the Paridæ and Sylvicolidæ agrees with the arrangement in Coues' Key and differs but little from the arrangement in the A. O. U. Check List. After placing the Paridæ below the Tanagridæ, Shufeldt remarks: "Indeed, were it not totally out of question to introduce a family in among the first five I have placed in the list, the Paridæ might hold a much more exalted rank, for in my opinion *the group of Tits and their immediate affines are birds of markedly high organization.* \* \* \* They possess unusually large brains for their size and there is just a possibility that *they are connected with the Corvidæ* through such species as *Perisoreus*; they show wonderful ingenuity in the construction of their nests, and the plumage of the young is almost identical with that of the parents, and finally, some of their kin (as *Chamæa*) have absolute scutellate podothecæ."<sup>(2)</sup> Since the *Paridæ* are birds of "markedly high organization" and since "there is just a possibility that they are connected with the *Corvidæ*," why not place them next to the *Corvidæ*? Judging by the type and relative size of the prosencephalon, that is where the group belongs.

In giving the *Fringillidæ* and *Icteridæ* a high rank this arrangement agrees with that of Shufeldt.

Placing the *Hirundinidæ* adjacent to the *Tanagridæ* agrees with Coues' Key and the A. O. U. Check List. Shufeldt places the swallows much lower in the scale, but admits that their exact affinities are not known.<sup>(3)</sup>

1 North American Passeres, by R. W. Shufeldt, M.P., C.M.Z.S., Journal of Morphology, vol. iii, pp. 107, 108.

2 Op. cit. p. 108.

3 "For a long time I was at a loss to know where to place the swallows (*Hirundinidæ*) and they have been crowded near the foot of the list, not that they have not a few points in their economy indicative of a certain degree of rather high specialization; still, although truly passerine birds, they are birds of comparatively small brains and their

It will be noticed that the Turdidæ have been placed lower in the scale than either the Tanagridæ, the Fringillidæ, or the Icteridæ. R. W. Shufeldt places the Turdidæ in about the same position. In defending his position, Mr. Shufeldt remarks, that the reduction of ten primaries to nine is an index of great specialization; he then adds: "The Tanagers show this feature; and it is a good one to hold them in the place which I have assigned them; moreover, it gives them precedence over the more lowly organized Turdidæ, which in realty should long ago have been recognized."<sup>(1)</sup>

#### RECAPITULATION.

1. The avian prosencephalon is large, but is not convoluted.
2. The avian epencephalon is well developed and transversely convoluted.

3. From the introduction of the class Aves until now, there has been a gradual retrograde evolution of the avian rhinencephalon. In the lowest type of birds, the rhinencephalon is double and projects beyond the cephalic extremity of the prosencephalon; in the highest type the rhinencephalon is single and does not project beyond the cephalic extremity of the prosencephalon.

4. In the lower types of avian brains the optic lobes are only partially covered by the prosencephalon; in the higher types the optic lobes are entirely covered.

5. During both the evolution of the class Aves and the differentiation of the families within it, the dorsal and lateral portions of the avian prosencephalon have grown caudad much more rapidly than the ventral and mesal portions. This has caused the caudal portion of each cerebral hemis-

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young differ in their plumage from the parents, and while we do not yet know the exact affinities of the Hirundinidæ, all the speculations in that quarter have been in the direction of associating them with groups of recognized low type of organization." Op.cit., p.110.

Although the brain of the Hirundinidæ may be relatively small, yet it is as highly developed as the brain of either the Tanagridæ or Icteridæ. C. H. T.

<sup>1</sup> Op. cit., p. 109.

phere to revolve towards the meson and at the same time to gradually cover the optic lobes.

6. The avian brain has a taxonomic value of great importance. So far, at least, as major groups are concerned, a classification based upon it alone agrees in all essentials with those that are based upon a careful study of all the structural elements.

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### III.—HISTOLOGY OF THE CEREBRUM.

*Rhinencephalon* (Plate VII, Figs. 6, 8, 10.) — Passing ental we meet in succession the following zones:

1. A superficial fibre zone, from the cephalic portion of which projects the olfactory nerve.

2. A gelatinous zone, in which the olfactory fibres appear to become knotted. In about the middle of this zone there is a narrow ring of small dense clusters of Deiter's corpuscles.

3. A clear zone containing a few scattered Deiter's corpuscles. Near the ental portion of this zone, there is a ring of nerve cells. My sections do not enable me to describe with certainty the structure of these cells. They appear to be of two sorts, fusiform or flask-shaped and rhinomorphic.<sup>(1)</sup> The fusiform cells, although smaller, resemble the fusiform cells of the prosencephalon. The rhinomorphic cells appear to be small modified pyramidal cells. The fusiform or flask-shaped cells are the prevailing type (Plate VII, Fig. 9). In most of my sections I have not seen any rhinomorphic cells. When they were present, they appeared to be scattered among the other cells.

4. A dense zone of Deiter's corpuscles.

5. A row of epithelium cells lining the ventricle. Where there is no olfactory ventricle this zone is necessarily absent.

*Ventricle* (Plate VII, Fig. 5.)—In all the bird brains examined, a narrow projection of the lateral ventricle extends

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<sup>1</sup> A. BUMM thinks that all of the nerve cells in the olfactory lobes are pyramidal. Op. cit., p. 450.

towards the rhinencephalon. When there is only one olfactory lobe this projection terminates in the olfactory crus. When two olfactory lobes are present, an extension of this projection enters each olfactory lobe and expanding, forms the olfactory ventricle.

#### PROSENCEPHALON.

*Ventricle* (Plate V, Figs. 2, 3, 6, 7; Plate VI, Figs. 3-5, 8, 10; Plate VII, Figs. 1-5, 7).—For convenience the ventricle may be divided into the following parts:

1. A narrow cavity, which is approximately parallel to the meson.
2. A lateral expansion of this cavity. This expansion curves over the dorsal portion of the axial lobe.
3. A common expansion of both of the above cavities. This expansion curves around the caudad portion of the axial lobe, and then turning, passes cephalad as far as the crura cerebri.

Thus a large portion of the caudad part of the axial lobe of each hemisphere is surrounded on all sides, excepting the cephalic and lateral, by the ventricle; while a small portion of the dorsal part of the axial lobe of each hemisphere is surrounded on all sides, excepting the ventral, by the ventricle.

The first part of this ventricle is, approximately, a triangle, with its base near the dorsal surface and its apex near the ventral surface of the prosencephalon. This cavity lies near the meson, but is not parallel to it. Near the dorsal surface of the prosencephalon it is diverted laterad by a local thickening of the cephalad portion of the mesal wall of the ventricle. At the same level, but near the caudad extremity of the prosencephalon, a local swelling of the dorsal portion of the mesal wall of the ventricle causes a laterad displacement of the ventricle. Slightly caudad to this place a small convex portion of the axial lobe projects into the ventricle. The two above-mentioned swellings of the mesal wall of the ventricle are connected by a narrow



neck. Ventrad to this neck another local swelling of the wall of the ventricle diverts the ventricle from the meson. Ventrad to this level the displaced ventricle does not return to its former proximity to the meson.

The second division of the ventricle is parallel to the dorsal surface of that hemisphere in which it is found.

*Divisions.*—For convenience the prosencephalon has been divided into three regions: the basal region, the mantle and the axial region. The basal region is that portion of the base of the prosencephalon which lies between the caudad extremity of the ventro-lateral tuber and the olfactory crura. It is histologically distinct from the remainder of the brain. In it nerve cells are either entirely absent or else represented by what Professor Herrick has termed rhinomorphic cells. The outer portion of the remainder of each hemisphere is called the mantle, while the inner portion is called the axial region. Along the mesal, dorsal and caudal portions of the hemisphere the mantle is separated from the axial region by the lateral ventricle. Elsewhere these two regions of the brain are distinguished by histological characteristics.

#### THE MANTLE.

In the mantle the nerve cells are not distributed promiscuously, but they are aggregated in distinct and constant localities. The brains of several different groups of birds have been examined, and in all cases the above statement has proved correct. More than that; in the prosencephalon of different birds, corresponding areas are supplied with similar cells. In the reptilian brain, according to Prof. C. L. Herrick, this is also true. In his paper on the cerebrum of the Lizard<sup>(1)</sup>, Prof. Herrick has called each of these cell clusters a nidulus and that portion of the hemisphere in which the cluster is found, a lobe. He has named each nidulus, and to each lobe he has given the name of the contained nidulus.

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<sup>1</sup> See "Topography and Histology of the Brains of Certain Reptiles," by Prof. C. L. Herrick. *Supra* p. 14.

Omitting the lenticular nidulus and lobe, I have found in the bird brain homologues of all the mantle niduli and lobes described in Prof. Herrick's paper.

*Divisions.*—For convenience the mantle has been divided into two divisions, a mesal and a lateral division. The mesal division is that portion of the mantle which lies mesad of the lateral ventricle. The remainder of the mantle constitutes the lateral division. Each division contains three lobes. In describing these lobes, I shall begin at the cephalic extremity of the mesal division and pass caudad through the mesal to the lateral division. Then I shall turn and pass cephalad through the lateral division to the starting point.

*Fronto-median Lobe.*—This lobe constitutes the cephalad portion of the mesal division of the mantle. It is the development of this lobe that causes the cephalad portion of the ventricle to be diverted from the meson. (Plate VI, Figs. 3, 5; F. M. L.) The ental boundary of this lobe is formed by the lateral ventricle; the mesal boundary is formed by the fissura longitudinalis; the dorsal portion of the cephalad boundary is formed by the frontal lobe, while the ventral portion of the same boundary is at the cephalad extremity of the prosencephalon. Near the dorsal surface of the hemisphere a projection of the frontal lobe is wedged in between the fronto-median lobe and the meson.

*Form and Size.*—This lobe is about twice as long as its greatest width and both horizontal and transverse sections of it are sub-triangular in outline. Dorsad and cephalad the lobe is quite wide, but while passing entad it becomes very narrow.

Near the dorsal surface of the brain the narrow caudad portion of the fronto-median lobe fuses with the narrow cephalad portion of the occipital lobe. Thus we have a narrow neck connecting two larger areas. (Plate VI, Fig. 3.) Ventrad to this neck the fronto-median lobe is connected by a narrow strip of brain substance to the intra-ventricular lobe.

*Structure.*—Passing laterad from the fissura longitudinalis to the ventricle, the fronto-median lobe is composed of three parts:

1. Bordering the meson, a narrow cell-less fibre layer.
2. A wider, inner portion containing nerve cells. This is the *fronto-median nidulus*. This nidulus is composed of a large number of irregularly arranged fusiform or flask cells, among which are distributed numerous Deiter's corpuscles. These flask cells are about twenty-five micro-millimetres wide. They stain faintly and have a clear, granular, sub-spherical nucleus and a dense nucleolus. The nucleus is quite large, being at least half as wide as the cell (Plate VIII, Fig. 2).

3. Bordering the ventricle, a narrow gelatinous layer of closely packed Deiter's corpuscles.

*Intra-ventricular Lobe* (Plate V, Fig. 6; Plate VII, Fig. 5).—This lobe occupies the middle portion of the mesal division of the mantle. It constitutes that local swelling of the mantle which lies ventrad to the fronto-median and occipital lobes. Cephalad and dorsad this lobe is connected by a narrow sheet of brain substance with the fronto-median and occipital lobes. This connecting sheet does not contain nerve cells, but it is moderately supplied with Deiter's corpuscles. The mesal boundary of this lobe is formed by the fissura longitudinalis. The majority of the ental boundary is formed by the lateral ventricle, the remainder by the axial region of the hemisphere.

Transverse sections of this lobe are sub-triangular, while horizontal sections may be either sub-triangular or diamond-shaped. Cephalad and dorsad this lobe is quite narrow, but while passing caudad and ventrad it gradually widens.

*Structure.*—Like the fronto-median, this lobe is composed of three portions:

1. Bordering the meson, a dense layer of slender fusiform cells. These cells are about three micro-millimetres wide and from 13 to 16 micro-millimetres long. Although fusi-

form in shape, these cells stain densely and have a dense nucleus. They lie in a fibre tract and have their major axes parallel to the meson and to the base of the prosencephalon (Plate VIII, Fig. 11).

2. A wider, inner portion, containing nerve cells. This is the *intra-ventricular nidulus*. It is composed of a large number of irregularly arranged gibbous, fusiform or flask cells, among which are distributed numerous Deiter's corpuscles. These fusiform cells are about three micro-millimetres wide and from 9 to 13 micro-millimetres long. They stain faintly and have a large, clear, granular sub-spherical nucleus and a dense nucleolus (Plate VIII, Fig. 11).

3. Extending along the ventricle, a narrow border of slender densely stained fusiform cells. Histologically these cells resemble the cells that extend along the meson. They vary in length from 10 to 13 micro-millimetres. Like the cells along the meson, their major axes are parallel to the meson and to the base of the brain.

*Occipital Lobe.*—This lobe constitutes the caudad portion of the mesal division of the mantle (Plate VI, Fig. 3; Plate VII, Fig. 5; O. L). It is the development of this lobe which causes the local swelling in the caudad portion of the mesal wall of the ventricle. The mesal boundary of this lobe is formed by the fissura longitudinalis, the lateral by the ventricle, while the caudad is coincident with a portion of the caudad surface of the hemisphere.

Horizontal sections of this lobe are crescent-shaped, while transverse sections are sub-triangular. Dorsad this lobe is quite wide, but while passing ventrad it gradually becomes narrow.

*Structure.*—This lobe also consists of three layers:

1. Along the mesal border there is a narrow cell-less layer containing fibres.

2. An inner portion containing nerve cells. This is the *occipital nidulus*. It consists of a large number of fusiform or flask cells, among which are distributed numerous Deiter's



corpuscles. These nerve cells are faintly stained and have a large, clear, granular, sub-spherical nucleus and a dense nucleolus. They are about seven micro-millimetres wide and from 13 to 15 micro-millimetres long.

3. Extending along the ventricle, a narrow gelatinous layer of Deiter's corpuscles.

*Parieto-occipital Lobe* (Plate VI, Figs. 1, 5; P. O. L).—

This lobe constitutes the caudad portion of the lateral division of the mantle. It forms the greater part of the caudad portion of each hemisphere and extends from the occipital lobe almost to the caudo-lateral border of the prosencephalon. Entad this lobe is bounded by the basi-occipital lobe and the corpus striatum, laterad it is bounded by the parieto-frontal lobe, ectad it is superficial. In some types the lateral ventricle penetrates this lobe.

In the avian prosencephalon the parieto-occipital lobe is much nearer the meson than is the corresponding lobe of the reptilian brain.<sup>(1)</sup> It is now almost universally admitted that birds and reptiles have been evolved from the same primitive group of vertebrates. If this be true, a mesal revolution of the caudad portion of each hemisphere is the only phenomenon that consistently accounts for the mesal position of the parieto-occipital lobe in the avian brain.

*Structure.*—This lobe consists of the following parts:

1. A narrow outer cell-less layer of free cortex.
2. A wide, irregular, inner layer of nerve cells. This is the *parieto-occipital nidulus*. It consists of a large number of Deiter's corpuscles and large pyramidal cells. These cells vary in length from 22 to 26 micro-millimetres. Their sides are either convex or straight. The apex of each cell is extended into a long process, while the base is supplied with several shorter processes. The apex process is often several times as long as the cell. These cells stain densely and have an elongated dense nucleus and denser nucleolus. Occasion-

<sup>1</sup> See Prof. Herrick's Paper on "Topography and Histology of the Brains of Certain Reptiles." *Supra* p. 14.

ally I have noticed cells with two well developed nuclei. Sometimes the nucleus is sub-spherical (Plate VIII, Fig. 1).

*Masked convolution.*—In the brain of Swainson's thrush (*Hylocichla swainsoni*) I have noticed a masked convolution. Near the mesal extremity of the parieto-occipital lobe and about half way between the dorsal and ventral surface of the prosencephalon a narrow projection of the parieto-occipital lobe extends entad. Within the axial portion of the brain this projection widens and form an ellipsoidal body. This small ellipsoidal body is histologically distinct from the region in which it is found, but it is histologically identical with the parieto-occipital lobe. The region around it is composed of fusiform nerve cells (Plate VIII, Fig. 12), while it is composed of pyramidal cells (Plate VIII, Fig. 6).

*Parieto-frontal Lobe* (Plate VI, Fig. 1, P. F. L.).—This lobe forms the middle portion of the lateral division of the mantle and extends from the parieto-occipital lobe to the fronto-median. It consists of two layers:

1. A narrow outer layer of free cortex.
2. A wider inner layer containing many Deiter's corpuscles and a few scattered nerve cells. This is the *parieto-frontal nidulus*. Near the cephalic portion of this lobe the cells are more abundant than elsewhere. These cells are pyramidal in outline and have either convex or straight sides. The apex is extended into a long process, while the base is supplied with several shorter processes. These cells stain densely and have an elongated dense nucleus and denser nucleolus.

*Frontal Lobe.*—This lobe forms the cephalad portion of the lateral division of the mantle. As has been mentioned above, a portion of it extends caudad between the cephalad portion of the fronto-median lobe and the meson. Dorsad it fuses with the parieto-frontal lobe and spreads over the greater portion of the dorsal surface of the hemisphere. Ventrad it is bounded by the fronto-median lobe (Plate VI, Figs. 1, 3, 5).

*Structure.*—This lobe consists of the following parts:

1. A narrow outer layer of free cortex.
2. A broader inner collection of nerve cells, among which is scattered a large number of Deiter's corpuscles. This is the *frontal nidulus*. These cells are pyramidal in outline and have convex or straight sides. They are from 12 to 16 micro-millimetres long and at the base are about six micro-millimetres wide. The apex is extended into a long process, while the base is supplied with several shorter processes. These cells stain densely and have a dense nucleus and a denser nucleolus. (Plate VIII, Fig. 4.)

#### AXIAL REGION.

The axial region is composed of two parts, the basi-occipital lobe and the corpus striatum.

*Basi-occipital Lobe.*—As has been mentioned above, the lateral division of each hemisphere is surrounded on the ventral, mesal and dorsal sides by the lateral ventricle. In the ventral part of this portion of the brain lies the basi-occipital lobe. The caudad and part of the mesal boundary of this lobe is formed by the parieto-occipital lobe. The ental and dorsal boundaries are formed by the corpus striatum.

*Structure.*—This lobe is composed of numerous Deiter's corpuscles, among which are distributed many fusiform or flask cells. These cells are about six micro-millimetres wide and from 12 to 16 micro-millimetres long. They stain faintly and contain a large, clear, subspherical nucleus and a dense nucleolus. In all probability these cells are undergoing rapid transverse subdivision (Plate VIII, Fig. 12). In the reptilian brain also, according to Prof. Herrick, the cells of this lobe are undergoing rapid subdivision. In that case, however, the subdivision is radial.<sup>(1)</sup>

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<sup>1</sup> See "Notes on the Brain of the Alligator," by Prof. C. L. Herrick, Journal of Cincinnati Society of Natural History, Vol. XII, Plate VII, Fig. 8.

In the reptilian brain Professor Herrick has considered this zone to be an area of great proliferation—an area in which cortex cells are developed.<sup>(1)</sup> In birds it may have a similar function.

*Minor nidulus.*—In the basi-occipital lobe, near the meson, and about half way between the dorsal and ventral surfaces of the hemisphere, there is a small, dense, ellipsoidal cluster of cells. I have called this cluster the minor nidulus. From this nidulus, the major axis of which is perpendicular to the major axis of the hemisphere, a tract of fibres passes to the anterior commissure (Plate VI, Fig. 5).

*Corpus striatum.*—The remainder of the axial region of the prosencephalon constitutes the corpus striatum.<sup>(2)</sup>

Histologically, the striatum is divided into two portions, the striated portion and the caudate portion. In position, these parts might be compared, respectively, to the lenticular and caudate nucleus of the mammalian striatum. I am not sure that these are true homologies, yet, as is stated below, there are two fibre layers which might, perhaps, be considered homologues of the internal and external capsules.

*Striated portion* (Plate VI, Fig. 8).—This portion lies in the ventral part of the prosencephalon and is adjacent to the crura cerebri. Passing from the crura cerebri into the cerebrum, we meet three divisions of the striated portion of the striatum:

1. A narrow band of dense clusters of Deiter's corpuscles. This band is, approximately, perpendicular to the entering

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1 "The great bulk of the axial lobe—the portion which protrudes into the ventricle—is filled with similar flask cells, but these are curiously clustered in groups of two or multiples of two. The evidence that these cells are undergoing rapid increase by fission in this young animal is very conclusive. All stages of the process may be observed. It may be suggested that, if in the case of young animals this part of the brain is most actively multiplying cells, it is possible that the growth of the mantle (in which there is little material for rapid growth) may be in some way associated with this proliferation of cells, resulting in the increase of the mantle from its margins, as though the material were pushed up around the margin of the ventricle by a rapid growth within." Op. cit., p. 143

2 A. BUMM regards the whole of the axial portion of the brain as the homologue of the corpus striatum. Op. cit., p. 455.



peduncular tract, and extends caudo-laterad from a short distance cephalo-mesad of the cephalo-lateral extremity of the crura cerebri to about twice that distance caudo-laterad of that place. In traversing this band, the peduncular fibres pass between, not through, the dense clusters of Deiter's corpuscles (Plate VIII, Fig. 9).

2. A clear lenticular portion, which lies parallel to and entad of number one. The nerve cells in this portion are few and far between. They are of two sorts, flask-shape and pyramidal (Plate VIII, Fig. 7). The cells of the first type are large, gibbous, faintly stained, flask-shaped cells. They have a large, clear, sub-spherical nucleus and a dense nucleolus. The cells of the other type are elongated, densely stained pyramidal cells. They have an elongated dense nucleus and a denser nucleolus. In the meso-cephalad portion of this nidulus the flask cells predominate, while in the caudo-lateral portion the pyramidal predominate.

In traversing this portion, the peduncular fibres separate into parallel bands of approximately the same size (Plate VIII, Fig. 5).

3. A wide irregular portion, which consists chiefly of Deiter's corpuscles. Occasionally we find a fusiform cell, and near the meso-cephalad extremity of part one there is usually a cluster of small pyramidal cells.

After entering this part of the striatum, the peduncular fibres radiate in all directions.

*Caudate Portion.*—This is the largest division of the striatum.

*Form.*—Viewed from the side, the outline of this division is composed of the following curves:

1. A convex curve, which forms the cephalad boundary. This curve extends cephalo-ventrad from the dorsal extremity of this division to the cephalo-ventral extremity of the same.
2. A convex curve, which extends ventro-caudad from the ventral extremity of curve one to the caudo-ventral extremity of the lobe.

3. An undulating line, which passes, in general, dorso-caudad from the dorsal extremity of curve two to the dorsal extremity of this division. The ventral half of this curve is strongly concave, while the dorsal half is strongly convex.

Viewed from above, the outline of this division is composed of the following curves:

1. A convex curve, which extends cephalo-laterad from the mesal extremity of this division to the cephalo-mesal border of the same. This curve is formed by the ventricle.

2. An undulating line, which passes latero-cephalad from the extremity of curve one to the latero-cephalad border of this division. At its extremities this lobe is feebly convex, in the middle it is feeble concave.

3. A convex curve, parallel to the lateral surface of the hemisphere, which extends from the extremity of curve two to the caudo-lateral margin of this division.

4. An undulating line, which extends, approximately, mesad from this place to the beginning of curve one. The lateral one-tenth of this curve is slightly concave, the succeeding four-tenths is moderately convex, the next four-tenths is strongly concave, and the remaining one-tenth is almost straight.

*Cell structure.*—Histologically, this division of the striatum differs from all other parts of the brain. Some of the cells are fusiform, while others are sub-pyramidal; but the greater number are swollen and distorted and contain several nuclei (Plate VIII, Fig. 10). The numerous small cells, resembling Deiter's corpuscles, that are present in this part of the striatum are of the same size as the nuclei of the large cells. No other portion of the prosencephalon is so well supplied with blood-vessels. This suggests that this is an area of great activity. Evidently it has a special work to perform. Professor Herrick suggests that it may be an area where germinative corpuscles are produced.

The corpuscles of this region resemble Deiter's corpuscles in so many respects that one is tempted to believe that they

are identical. Both the white and the red corpuscles of the blood have special localities in which they are elaborated. Why may not Deiter's corpuscles have a special locality in which they are developed and from which they migrate in all directions? The numerous Deiter's corpuscles that are found in the vicinity lead one to suppose that the caudate portion of the striatum is such a locality.

Prof. His has shown that the original nerve cells develop from small corpuscles, the neuroblasts.<sup>(1)</sup> Why may not all nerve cells be formed in the same way? Why may not these so-called germinative corpuscles of the striatum be the neuroblasts of future nerve cells?

Whatever the function of these corpuscles, the evidence that they are produced in the caudate portion of the striatum is most conclusive. Anywhere within this part of the brain the one-fourth inch objective will reveal the whole process. Within its field of view may be observed cells of all sizes and ages. There is the normal cell with one nucleus and one nucleolus. Of the same size as this cell, but a little older, is the cell with one nucleus and two nucleoli. Then come cells of two, three and more nuclei. The size of the cells seems to endeavor to keep pace with the number of nuclei. This is not fully accomplished, but cells that contain eight or nine nuclei are two or three times the size of the original cells. Such a cell may be regarded an aged one. Its period of activity has passed. It becomes decrepit. Little by little it fades away, until eight or nine clustered nuclei are the only remains of its former greatness. These nuclei are not inactive. Soon they migrate to other parts of the brain, bearing within their walls the substance of the mother cell (Plate VIII, Fig. 10).

*Internal Capsule.*—Between the striated and caudate portions of the striatum there is a sheet of fibres that may be considered as the homologue of the internal capsule.

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1 Archiv für Physiologie und Anatomie, 1890.

*External Capsule.*—Near the cephalic boundary of the caudate portion of the striatum there is another sheet of fibres. This may be regarded as the homologue of the *external capsule*.

*Anterior Commissure.*—Immediately cephalad to the diencephalon and near the base of the prosencephalon the anterior commissure connects the two hemispheres of the avian brain (Plate VII, Fig. 3; Plate VI).

After leaving the crura the majority of the fibres of this commissure pass caudad and slightly dorsad into the basi-occipital lobe. These fibres keep near to the mesal surface of the hemisphere. In addition to these a few fibres appear to pass directly laterad. I have looked in vain for fibres passing from this commissure to the olfactory lobes.

*Corpus Callosum* (Plate VI, Fig. 2; Plate VII, Figs. 3, 7; C. C.).—This commissure lies caudad and dorsad to the anterior commissure. It is much smaller than the latter. Between the ventricle and the meson the fibres of the corpus callosum radiate towards the dorsal surface of the brain.<sup>(1)</sup>

*Peduncular Tracts.*—These tracts enter the prosencephalon by the crura cerebri. At the crura they are perpendicular to the longitudinal axis of the hemisphere. A few of these fibres pass cephalo-dorsad to the caudate portion of the striatum. These fibres pass mesad of the striated portion of the striatum, the remainder pass through it. As mentioned above, at this place the striatum is composed of several layers. Passing entad we meet in succession: (1) A layer containing dense clusters of Deiter's corpuscles; (2) A clear lenticular portion which contains two kinds of nerve cells; (3) A large area which is composed chiefly of Deiter's corpuscles. In each of these portions the course of the peduncular tracts is different. In the first the fibres pass

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<sup>1</sup> Most writers have said that birds do not have a corpus callosum, but A. Bumm, the most recent European student of the avian prosencephalon, affirms its existence in European birds. Op. cit., p. 462.



between the clusters of Deiter's corpuscles; in the second they separate into uniform parallel bundles; in the third they radiate in all directions.

*Tenia Thalami*.—Near the meson and dorsad to the peduncular tract, these fibres enter the prosencephalon. Immediately they turn dorsad, and, if I have traced them correctly, after passing dorsad for a short distance they turn laterad. After traversing about half the width of the hemisphere the tract again turns dorsad. Always keeping near the caudad extremity of the hemisphere, it continues dorsad and disappears near the dorsal surface of the brain.

*Tractus Bummi* (Plate VI, Figs. 7-9).—This tract originates in either the frontal or fronto-median lobe and passes caudo-ventrad through the intra-ventricular lobe. After passing beneath the anterior commissure it turns and passes ventro-latero-caudad to the crura cerebri. Penetrating the dorsal part of the crura it passes to the outer fibre layer of the tectum opticum. This tract does not decussate. It connects the mesal wall of the ventricle of one side of the brain to the optic lobe of the same side. To the best of my knowledge, A. Bumm<sup>(1)</sup> is the only one who heretofore has accurately described this tract. He called it, "Markbündle der strahligen Scheidewand." This name being too formidable for English readers, I have ventured to name this tract, after its discoverer, *Tractus Bummi*.

#### RECAPITULATION.

1. In addition to and distinct from the anterior commissure, there is a corpus callosum.
2. There is a fibre tract connecting the mesal division of the mantle with the optic lobe of the same side.
3. In different avian prosencephala corresponding areas are supplied with similar cells.
4. In the mantle and axial region of the procephalon there are two types of cells, fusiform and pyramidal.

<sup>1</sup> Op. cit., p. 451.

Cells of the first type are fusiform, or flask-shaped. They stain faintly, and contain a large, clear, granular, sub-spherical nucleus and a dense nucleolus.

The cells of the second type are pyramidal in form. They have straight or concave outlines and a broad base. The apex of the cell is extended into a long process, while the base is supplied with several shorter processes. These cells stain densely and have an elongated dense nucleus and a denser nucleolus.

5. The mesal division of the mantle contains fusiform cells only.

6. The lateral division of the mantle contains pyramidal cells only.

7. The corpus striatum contains both fusiform and pyramidal cells.

8. There is a portion of the avian striatum in which small cells, resembling Deiter's corpuscles, are developed.

9. In the brain there may be an entad projection of grey matter, without any external indication of a convolution.

TABLE I.—RHINENCEPHALON.

Orders.	Families.	Individuals.	Length.	Breadth.	Fused.	Project.	Partly imbedded.
PASSERES.	<i>Turdida.</i>	<i>Turdus migratorius.</i>	13	15	+	—	—
		<i>Turdus mustelinus.</i>			+	—	—
		<i>Mimus polyglottus.</i>	13	16	+	—	—
		<i>Mimus carolinensis.</i>	11	12	+	—	—
		<i>Harporynchus rufus.</i>	12	12	+	—	—
	<i>Parida.</i>	<i>Sialia sialis.</i>			+	—	—
		<i>Lophophanes bicolor.</i>	15	15	+	—	—
	<i>Sittida.</i>	<i>Sitta carolinensis.</i>			+	—	—
	<i>Sylviolidae.</i>	<i>Dendroca pinus.</i>	10	8	+	—	—
		<i>Oporornis formosa.</i>			+	—	—
	<i>Tanagridae.</i>	<i>Pyrranga rubra.</i>	14	14	+	—	—
	<i>Hirundinidae.</i>	<i>Hirundo erythrogastra horreorum.</i>	16		+	—	—
	<i>Vireonidae.</i>	<i>Vireo philadelphicus.</i>			+	—	—
	<i>Fringillidae.</i>	<i>Passer domestica.</i>			+	—	—
		<i>Astragalinus tristis.</i>			+	—	—
		<i>Spizella domestica.</i>	10	10	+	—	—
		<i>Zamelodia ludoviciana.</i>	12	17	+	—	—
		<i>Passerina cyanea.</i>	11	13	+	—	—
	<i>Icteridae.</i>	<i>Cardinalis virginia.</i>			+	—	—
		<i>Pipilo erythrophthalmus.</i>			+	—	—
		<i>Agelaius phoeniceus.</i>	11	11	+	—	—
		<i>Sturnella magna.</i>	10	10	+	—	—
		<i>Icterus galbula.</i>			+	—	—

TABLE I.—RHINENCEPHALON (*Continued*).

Orders.	Families.	Individuals.	Length.	Breadth.	Fused.	Project.	Partly imbedded.
PASSERES.	<i>Icteridae.</i>	<i>Quiscalus americanus.</i>	10	10	+	—	+
	<i>Corvidae.</i>	<i>Corvus americanus.</i> <i>Cyanocitta cristata.</i>	6		+	—	++
	<i>Tyrannidae.</i>	<i>Tyrannus carolinensis.</i> <i>Myiarchus cinerascens.</i> <i>Contopus virens.</i>	11 11 8	11 12 8	+(?) +(?) +(?)	—	+
	<i>Cuculidae.</i>	<i>Coccyzus americanus.</i>	12	16	—	—	+
PICARIE.	<i>Picidae.</i>	<i>Picus pubescens.</i> <i>Melanerpes erythrocephalus.</i> <i>Colaptes auratus.</i>	10 11 10	20	— — —	—	++
RAPTORES.	<i>Strigidae.</i>	<i>Bubo virginianus.</i>	9	9	—	—	—
COLUMBE.	<i>Meleagrididae.</i>	<i>Meleagris gallipavo.</i>	11	15	—	+	—
	<i>Tetraonidae.</i>	Domestic fowl.	13		—	+	—
LIMICOLE.	<i>Scopacidae.</i>	<i>Gallinago wilsoni.</i> <i>Tringoides macularius.</i>	6		—	++	+
	<i>Ardeidae.</i>	<i>Ardea herodias.</i> <i>Butorides virescens.</i> <i>Botaurus mugitans.</i>	18 14 14	19 14	— —	++ ++	— —
LAMELLIROSTRES.	<i>Anatidae.</i>	Domestic goose.			—	—	—



TABLE II.—PROSENCEPHALON.

Orders.	Families.	Individuals.	Length.	Breadth.	Depth.	V. L. B. D.	Dorsal fissure median.	Dorsal fissure frontal.	Ventro-lateral tuber.	Ventro-medial tuber.	Ventro-frontal tuber.
PASSERES.	<i>Turdidae.</i>	<i>Turdus migratorius.</i>	78	104	52	74.99	—	+	+	+	—
		<i>Turdus mustelinus.</i>	76	111	50	74.99	—	+	+	+	—
		<i>Mimus polyglottus.</i>	81	106	50	75.43	—	+	+	+	—
		<i>Mimus Carolinensis.</i>	77	93	56	73.73	—	+	+	+	—
		<i>Harporhynchus rufus.</i>	75	106	53	74.97	—	+	+	+	—
		<i>Sialia stalis.</i>									
	<i>Paridae.</i>	<i>Lophophanes bicolor.</i>	92	123	54	84.85	—	+	+	+	—
	<i>Sittidae.</i>	<i>Sitta Carolinensis.</i>					—	+	+	+	—
	<i>Sylviolidae.</i>	<i>Dendroica pinus.</i>	87	108	62	83.45	—	+	+	+	—
		<i>Oporornis formosa.</i>					—	+	+	+	—
	<i>Tanagridae.</i>	<i>Pyrranga rubra.</i>	79	107	57	78.39	—	+	+	+	—
	<i>Hirundinidae.</i>	<i>Hirundo erythrogastra</i> [horreorum.	79	125	50	78.44	—	+	+	+	—
	<i>Vireonidae.</i>	<i>Vireo philadelphicus.</i>	79	117	54	79.33	—	+	+	+	—
	<i>Fringillidae.</i>	<i>Passer domestica.</i>	91	111	55	82.21	—	+	+	+	—
		<i>Astragalinus tristis.</i>	85	116	57	82.52	—	+	+	+	—
		<i>Spizella domestica.</i>	86	115	54	81.13	—	+	+	+	—
		<i>Zamelodia ludoviciana</i>	84	112	51	79.41	—	+	+	+	—
		<i>Passerina cyanea.</i>	91	113	54	82.19	—	+	+	+	—
		<i>Cardinalis virginiana.</i>	89	108	56	81.35	—	+	+	+	—
	<i>Icteridae.</i>	<i>Pipilo erythrophthalmus.</i>	85	95	53	75.40	—	+	+	+	+
		<i>Agelaius phoeniceus.</i>	81	109	54	78.11	—	+	+	+	—
		<i>Sturnella magna.</i>	81	112	51	77.35	—	+	+	+	—
		<i>Icterus galbula.</i>					—	+	+	+	—
		<i>Quiscalus purpureus.</i>					—	+	+	+	—

TABLE II.—PROSENCEPHALON (Continued).

Orders.	Families.	Individuals.	Length.	Breadth.	Depth.	$\frac{3}{V}$ , L. B. D.	Dorsal fissure median.	Dorsal fissure frontal.	Ventro lateral tuber.	Ventro median tuber.	Ventro frontal tuber.
PASSERES.	<i>Corvidæ.</i>	Corvus americanus. Cyanocitta cristata.	93	125	68	92.46	—	+	+	+	+
	<i>Tyrannidæ.</i>	Tyrannus carolinensis. Myiarchus cinerescens Contopus virens.	66 68 61	96 97 101	44 49 45	65.34 68.63 65.21	—	+	+	+	—
PICARIE.	<i>Cuculidæ.</i>	Coccyzus americanus.	59	93	45	62.74	+	—	+	+	+
	<i>Picidæ.</i>	Picus pubescens. Melanerpes erythro- cephalus.	77 75 86	102 105 105	58 60 55	76.94 77.89 74.90	+	—	+	+	+
RAPTORES.	<i>Strigidæ.</i>	Colaptes auratus. Bubo virginianus.	73	115	61	78.18	—	+	+	+	+
COLUMBÆ.											
GALLINÆ.	<i>Meleagrididæ.</i>	Meleagris gallipavo.	67	93	44	64.96	—	+	+	+	+
	<i>Tetraonidæ.</i>	Domestic fowl.	61	100	46	65.46	—	+	+	+	+
LIMICOLÆ.	<i>Scelopariidæ.</i>	Gallinago wilsoni. Tringoides macularius	77	92	60	75.18	+	—	+	+	+
HERODIONES.	<i>Ardeidæ.</i>	Ardea herodias. Butorides virescens. Botaurus mugitans.	59 61 55	77 83 77	44 52 45	58.43 64.03 57.90	—	+	+	—	—
LAMELLIROSTRES.	<i>Anatidæ.</i>	Domestic goose.					+	—	—	—	—

TABLE III.—MESENCEPHALON.

Orders.	Families.	Individuals.	Length.	Breadth.	Covered.
PASSERES.	<i>Turdidae.</i>	<i>Turdus migratorious.</i>	32	28	+
		<i>Turdus mustelinus.</i>	35	24	
		<i>Mimus polyglottus.</i>	37	25	+
		<i>Mimus carolinensis.</i>	30	19	+
		<i>Harporhynchus rufus.</i>	29	24	+
		<i>Sialia sialis.</i>			
	<i>Paridae.</i>	<i>Lophophanes bicolor.</i>	46	35	+
		<i>Sitta carolinensis.</i>			+
	<i>Sylviolidae.</i>	<i>Dendroeca pinus.</i>	37	31	+
		<i>Oporornis fermosa.</i>			+
	<i>Tanagridae.</i>	<i>Pyranga rubra.</i>	36	29	+
	<i>Hirundinidae.</i>	<i>Hirundo erythrogastra horreorum.</i>	42	25	+
	<i>Vireonidae.</i>	<i>Vireo philadelphicus.</i>	33	29	+
	<i>Fringillidae.</i>	<i>Passer domestica.</i>	39	25	+
<i>Astragalinus tristis.</i>		34	27	+	
<i>Spizella domestica.</i>		37	26	+	
<i>Zamelodia ludoviciana.</i>		35	24	+	
<i>Passerina cyanea.</i>		36	28	+	
<i>Cardinalis virginiana.</i>		38	25	+	
<i>Pipilo erythrophthalmus.</i>				+	
<i>Ageleus phœniceus.</i>		31	26	+	
<i>Sturnella magna.</i>				+	
<i>Icterus galbula.</i>		30	24	+	
<i>Quiscalus purpureus.</i>		35	25	+	

TABLE III.—MESENCEPHALON (Continued).

Orders.	Families.	Individuals.	Length.	Breadth.	Covered.
PASSERES.	<i>Corvidæ.</i>	Corvus americanus. Cyanocitta cristata.	44	25	— —
	<i>Tyrannidæ.</i>	Tyrannus carolinensis. Myiarchus cinerescens. Contopus virens.	37 39 40	30 29 28	— — — (?) (?) (?)
	<i>Cuculidæ.</i>	Coccyzus americanus.	32	26	—
	<i>Picidæ.</i>	Picus pubescens. Melanerpes erythrocephalus. Colaptes auratus.	32 30 30	25 26 21	— — —
RAPTORES.	<i>Strigidæ.</i>	Bubo virginianus.	29	21	—
COLUMBÆ.		Columba livia.			—
GALLINÆ.	<i>Meleagrididæ.</i>	Meleagris gallipavo.	33	26	—
	<i>Tetraonidæ.</i>	Domestic fowl.	33	25	—
LIMICOLÆ.	<i>Scolopacidæ.</i>	Gallinago wilsoni. Tringoides macularius.	35	31	—
HERODIONES.	<i>Ardeidæ.</i>	Ardea herodias. Butorides virescens. Botaurus mugtans.	29 29 28	21 24 23	— — —
LAMELLIROSTRES.	<i>Anatidæ.</i>	Domestic goose.			—



TABLE IV.—EPENCEPHALON.

Orders.	Families.	Individuals.	Length.	Breadth.	Depth.
PASSERES.	<i>Turdidae.</i>	<i>Turdus migratorius.</i>	37	37	46
		<i>Turdus mustelinus.</i>	34	38	38
		<i>Mimus polyglottus.</i>	28	37	47
		<i>Mimus carolinensis.</i>	35	41	42
		<i>Harporhynchus rufus.</i>	29	35	41
		<i>Sialia stalis.</i>			
	<i>Paridae.</i>	<i>Lophophanes bicolor.</i>	19	46	46
	<i>Sittidae.</i>	<i>Sitta carolinensis.</i>			
	<i>Sylviolidae.</i>	<i>Dendroica pinus.</i>	35	46	46
		<i>Oporornis formosa.</i>			
	<i>Troglodytidae.</i>	<i>Pyrrhula rubra.</i>	42	43	50
	<i>Hirundinidae.</i>	<i>Hirundo erythrogastra horreorum.</i>	42	50	50
	<i>Vireonidae.</i>	<i>Vireo philadelphicus.</i>	44	41	46
	<i>Fringillidae.</i>	<i>Passer domesticus.</i>	44	48	44
		<i>Astragalinus tristis.</i>	43	50	42
		<i>Spizella domestica.</i>	39	48	40
		<i>Zamelodia ludoviciana.</i>	38	35	43
		<i>Passerina cyanea.</i>	37	45	37
		<i>Cardinalis virginiana.</i>	44	48	37
		<i>Pipilo erythrophthalmus.</i>			
	<i>Icteridae.</i>	<i>Agelaius phoeniceus.</i>	37	42	37
		<i>Sturnella magna.</i>			
		<i>Icterus galbula.</i>	42	38	41

TABLE IV.—EPENCEPHALON (Continued).

Orders	Families.	Individuals.	Length.	Breadth.	Depth.
PASSERES.	<i>Icterida.</i>	<i>Quiscalus purpureus.</i>	37	38	42
	<i>Corvida.</i>	<i>Corvus americanus.</i>	35	33	44
	<i>Tyrannida.</i>	<i>Tyrannus carolinensis.</i>	37	44	41
		<i>Myiarchus cinerascens.</i>	43	50	43
PICARIE.	<i>Cuculida.</i>	<i>Contopus virens.</i>	45	46	36
		<i>Coccygus americanus.</i>	47	45	36
	<i>Picida.</i>	<i>Picus pubescens.</i>	44	44	44
		<i>Melanerpes erythrocephalus.</i>	40	44	48
RAPTORES.	<i>Strigida.</i>	<i>Colaptes auratus.</i>	38	47	38
		<i>Bubo virginianus.</i>	39	42	39
COLUMBÆ.					
GALLINÆ.	<i>Meleagridida.</i>	<i>Meleagris gallipavo.</i>	56	48	41
	<i>Tetraonida.</i>	Domestic fowl.	46	42	38
LIMICOLÆ.	<i>Scolopacida.</i>	<i>Gallinago wilsoni.</i>	31	46	46
	<i>Ardeida.</i>	<i>Tringoides macularius.</i>			
HERODIONES.		<i>Ardea herodias.</i>	43	38	32
	<i>Butorides virescens.</i>	35	45	31	
	<i>Botaurus mugilans.</i>		38	28	
LAMELLIROSTRES.	<i>Anatida.</i>	Domestic goose.			

TABLE V.—METENCEPHALON.

Orders.	Families.	Individuals.	Length.	Breadth.	Depth.
PASSERES.	<i>Turdidae.</i>	<i>Turdus migratorius.</i>	38	35	18
		<i>Turdus mustelinus.</i>	35	29	13
		<i>Mimus polyglottus.</i>	41	37	25
		<i>Mimus carolinensis.</i>	34	34	16
		<i>Harporhynchus rufus.</i>	35	29	23
	<i>Paridae.</i>	<i>Sialia sialis.</i>			
		<i>Lophophanes bicolor.</i>	35	35	23
	<i>Sittidae.</i>	<i>Sitta carolinensis.</i>			
	<i>Sylviolidae.</i>	<i>Dendroica pinus.</i>	38	38	20
		<i>Oporornis formosa.</i>			
	<i>Tanagridae.</i>	<i>Pyrranga rubra.</i>	36	36	29
	<i>Hirundinidae.</i>	<i>Hirundo erythrogastra horreorum.</i>	42	50	33
	<i>Vireonidae.</i>	<i>Vireo philadelphicus.</i>	33	42	25
	<i>Fringillidae.</i>	<i>Passer domestica.</i>	40	30	26
		<i>Astragalinus tristis.</i>	33	42	23
		<i>Spizella domestica.</i>	36	41	27
		<i>Zamelodia ludoviciana.</i>	35	35	24
		<i>Passerina cyanea.</i>	36	36	27
	<i>Icteridae.</i>	<i>Cardinalis virginiana.</i>	37	31	25
		<i>Pipilo erythrophthalmus.</i>			
		<i>Agelaius phoeniceus.</i>	37	34	21
		<i>Sturnella magna.</i>			

TABLE V.—METENCEPHALON (*Continued*).

Orders.	Families.	Individuals.	Length.	Breadth.	Depth.
PASSERES.	<i>Icteridae.</i>	Icterus galbula.	30	35	19
		Quiscalus purpureus.	39	37	23
	<i>Corvidae.</i>	Corvus americanus.	38	38	21
	<i>Tyrannidae.</i>	Tyrannus carolinensis.	37	37	22
PICARIE.		Myiarchus cinerescens.	36	36	22
		Contopus virens.	36	34	24
	<i>Cuculidae.</i>	Coccyzus americanus.	37	33	21
	<i>Picidae.</i>	Picus pubescens.	37	38	19
RAPTORES.		Melanerpes erythrocephalus.	35	41	21
		Colaptes auratus.	40	32	23
	<i>Strigidae.</i>	Bubo virginiana.	39	39	26
COLUMBÆ.					
	<i>Meleagrididae.</i>	Meleagris gallipavo.	54	41	30
	<i>Trogonidae.</i>	Domestic fowl.	50	33	21
	<i>Scolopacidae.</i>	Gallinago wilsoni.	46	44	23
LIMICOLÆ.		Tringoides macularius.			
	<i>Ardeidae.</i>	Ardea herodias.	47	32	22
		Butorides virescens.	38	38	24
		Botaurus mugilans.	46	33	15
HERODIONES.					

TABLE VI.

PROS.		HUNLEY.		PARKER.	
A.—Greatest width of the prosencephalon more than 90 per cent. of the length of the brain.	(a) Olfactory lobes covered, fused and imbedded. Dorsal fissure lateral.	Optic lobes covered.	<i>Corvidæ</i> (92) <i>Paridæ</i> (84) <i>Sittidæ</i> <i>Sylviolidæ</i> (83) <i>Fringillidæ</i> (79-82) <i>Icteridæ</i> (75-78) <i>Vireonidæ</i> (79) <i>Troglonidæ</i> (78) <i>Hirundinidæ</i> (78) <i>Turdidæ</i> (73-75) <i>Tyrannidæ</i> (65-68)	CORACO- MORPH.E.	EGITHO- GNATHOUS.
	(b) Olfactory lobes covered, free and imbedded.	I. Optic lobes covered.  II. Optic lobes partly exposed	<i>Strigidæ</i> (78) <i>Picidæ</i> (76-77)  <i>Cuculidæ</i> (62)	EGITHO- MORPH.E.  EGITHO- GNATHOUS.	EGITHO- GNATHOUS.

A.—Greatest width of the prosencephalon more than 90 per cent. of the length of the brain.



TABLE VI. (*Continued*).

PROS.	HUXLEY.	PARKER.
<p>(c) Olfactory lobe project, subterminal. Intersection of dorsal fissure with the meson not visible from above.</p> <p>(d) Olfactory lobes project, terminal. Intersection of dorsal fissure with the meson visible from above.</p>	<p>CHARADRIOMORPHÆ. PERISTERMORPHÆ. ALECTEROMORPHÆ. PELAGIOMORPHÆ.</p> <p>CHENOMORPHÆ. CECOMORPHÆ.</p>	<p>SCHIZO-GNATHÆ. SAURO-GNATHÆ. SCHIZO-GNATHÆ.</p>
<p><i>B.</i>—Greatest width of the pre-encephalon less than 90 per cent. of the length of the brain.</p>	<p><i>Scolapacidae</i> (75) <i>Columbidae</i> <i>Domestic fowl</i> (65) <i>Melanerididae</i> (64) <i>Ardeidae</i> (58-64)*</p> <p><i>Anatidae</i>†</p> <p><i>Columbidae</i> <i>Laridae</i></p>	
	<p>Optic lobes exposed</p> <p>I. Optic lobes covered.</p> <p>II. Optic lobes partly exposed</p>	<p>SCHIZO-GNATHOUS.</p>

*B.*—Greatest width of the pre-encephalon less than 90 per cent. of the length of the brain.

The *Ardeidae* are *desmognathous*. The storks and cranes, however, are *schizognathous*.

† Professor Huxley says that some of the Anserine birds are *schizognathous* and that others are *desmognathous*. Professor Cones says that the *Anatidae* are *desmognathous*.

TABLE VII.

COUES.	A. O. U.	SHUFELDT.	$^3\sqrt{(L \times B \times D)}$
<i>Turdidæ.</i>	<i>Turdidæ.</i>	<i>Corvidæ.</i>	<i>Corvidæ</i> (92)
<i>Paridæ.</i>	<i>Sylviidæ.</i>	<i>Icteridæ.</i>	<i>Paridæ</i> (84)
<i>Sylvicolidæ.</i>	<i>Paridæ.</i>	<i>Fringillidæ.</i>	<i>Sylvicolidæ</i> (83)
<i>Tanagridæ.</i>	<i>Virconidæ.</i>	<i>Tanagridæ.</i>	<i>Fringillidæ</i> (78-82)
<i>Hirundinidæ.</i>	<i>Hirundinidæ.</i>	<i>Paridæ.</i>	<i>Icteridæ</i> (75-78)
<i>Virconidæ.</i>	<i>Tanagridæ.</i>	<i>Turdidæ.</i>	<i>Virconidæ</i> (79)
<i>Fringillidæ.</i>	<i>Fringillidæ.</i>	<i>Sylviidæ.</i>	<i>Tanagridæ</i> (78)
<i>Icteridæ.</i>	<i>Icteridæ.</i>	<i>Virconidæ.</i>	<i>Hirundinidæ</i> (78)
<i>Corvidæ.</i>	<i>Corvidæ.</i>	<i>Hirundinidæ.</i>	<i>Turdidæ</i> (73-75)
<i>Tyrannidæ.</i>	<i>Tyrannidæ.</i>	<i>Tyrannidæ.</i>	<i>Tyrannidæ</i> (65-68)

## PLATE V.

*Fig. 1.* Brain of *Bubo virginianus*. Lateral view. *D.F.*, dorsal fissure; *F.M.*, ventro-frontal tuber.

*Figs. 2, 3, 11, 12.* Transverse sections of the prosencephalon of *Sialia sialis*. *C.P.*, proliferating area of the corpus striatum; *I.V.L.*, intra-ventricular lobe; *O.L.*, occipital lobe; *Rh.*, rhinencephalon.

*Fig. 4.* Brain of *Botaurus mugitans*. Lateral view. The Roman numerals indicate the cranial nerve roots.

*Fig. 5.* Brain of domestic goose. Dorsal view. *D.F.*, dorsal fissure.

*Fig. 6.* Brain of *Butorides virescens*. Dorsal view. *D.F.*, dorsal fissure; *F.*, flocculus; *Op.*, optic lobes.

*Fig. 7.* Brain of *Ageleus phæniceus*. Ventral view. *D.F.*, dorsal fissure; *T.*, a diamond-shaped depression which marks the caudad extremity of the brain.

*Fig. 8.* Brain of *Coccygus americanus*. Dorsal view. *D.F.*, dorsal fissure.

*Fig. 9.* Brain of *Botaurus mugitans*. Ventral view. The Roman numerals indicate the cranial nerve roots.

*Fig. 10.* Brain of *Colaptes auratus*. Dorsal view. *D.F.*, dorsal fissure; *Pr.*, prosencephalon.

*Fig. 13.* Brain of *Colaptes auratus*. Ventral view. The Roman numerals indicate the position of the cranial nerve roots. *Fl.*, flocculus;

*Mt.*, metencephalon; *O.T.*, optic tract; *Rh.*, rhinencephalon; *V.F.T.*, ventro-frontal tuber; *V.L.T.*, ventro-lateral tuber; *V.M.F.*, ventro-median fissure; *V.M.T.*, ventro-median tuber.

All surface views are drawn to the same scale.

#### PLATE VI.

*Figs. 1, 3, 4, 5, 8, 10.* Horizontal longitudinal sections of the brain of *Hylocichla swainsoni*, beginning near the dorsal surface. *A.C.*, anterior commissure; *C.P.*, proliferating area of the corpus striatum; *F.L.*, frontal lobe; *F.M.L.*, fronto-median lobe; *O.L.*, occipital lobe; *P.F.L.*, parieto-frontal lobe; *Pd.*, peduncular tracts; *P.O.L.*, parieto-occipital lobe; *T.B.*, *tractus Bummi*.

*Fig. 2.* Transverse section of a portion of the prosencephalon of *Sialia sialis*, showing the corpus callosum and the anterior commissure. *A.C.*, anterior commissure; *C.C.*, corpus callosum.

*Fig. 6.* Longitudinal-perpendicular section of the brain of *Sialia sialis*. Taken through the crura cerebri. *C.P.*, proliferating area of the corpus striatum.

*Figs. 7, 9.* Horizontal longitudinal sections of a portion of the prosencephalon of *Harporhynchus rufus*, for comparison with *Figs. 5, 8, 10.* *T.B.*, *tractus Bummi*.

#### PLATE VII.

*Figs. 1, 2, 4.* Longitudinal perpendicular sections of the brain of *Sialia sialis*. *C.P.*, proliferating area of the corpus striatum; *Ep.*, epencephalon; *Icp.*, internal capsule; *M.V.*, ventricle of the optic lobe; *T.Th.*, *tænia thalami*.

*Fig. 3.* Mesal section of the brain of *Meleagris gallipavo*; *A.C.*, anterior commissure; *C.C.*, corpus callosum; *O.ch.*, optic chiasm; *Pn.*, pineal body; *Rh.*, rhinencephalon; *S.C.*, superior commissure.

*Figs. 5, 7.* Horizontal longitudinal sections of the brain of *Meleagris gallipavo* to the same scale as *Fig. 3.* *A.C.*, anterior commissure; *C.C.*, corpus callosum; *O.L.*, occipital lobe.

*Fig. 6.* Transverse section of the rhinencephalon of the goose; *a.*, outer layer of olfactory fibres; *b.*, gelatinous layer; *c.*, dense clusters of Deiter's corpuscles in the gelatinous layer; *d.*, clear granular layer; *e.*, specific olfactory cells; *f.*, dense cluster of Deiter's corpuscles; *g.*, epithelium of the ventricle.

*Fig. 8.* Transverse section through the middle of the rhinencephalon of *Passer domestica*. *a.*, outer layer of olfactory fibres; *b.*, gelatinous layer; *d.*, clear granular layer; *e.*, specific olfactory cells; *f.*, dense cluster of Deiter's corpuscles.

*Fig. 9.* Nerve cells from the rhinencephalon of *Hylocichla swainsoni*.

*Fig. 10.* Transverse section through the rhinencephalon of *Hylocichla swainsoni*. Nomenclature the same as in *Fig. 8.*

## PLATE VIII.

*Fig. 1.* Portion of the parieto-occipital lobe of *Hylocichla swainsoni*.

*Fig. 2.* Portion of the fronto-median lobe of *Hylocichla swainsoni*.

*Fig. 3.* Portion of the occipital lobe of *Hylocichla swainsoni*.

*Fig. 4.* Portion of the frontal lobe of *Hylocichla swainsoni*.

*Fig. 5.* Portion of the striated portion of the corpus striatum of *Hylocichla swainsoni*, showing parallel bands of peduncular fibres.

*Fig. 6.* Highly magnified pyramidal cells from the parieto-occipital nidulus of *Hylocichla swainsoni*.

*Fig. 7.* Highly magnified cells from the corpus striatum of *Hylocichla swainsoni*.

*Fig. 8.* Highly magnified fusiform or flask cells from the fronto-median lobe of *Hylocichla swainsoni*.

*Fig. 9.* Portion of the striated portion of the corpus striatum of *Hylocichla swainsoni* showing peduncular fibres passing around a cluster of Deiter's corpuscles.

*Fig. 10.* A highly magnified section of the proliferating portion of the corpus striatum. 1, original cell, with one nucleus and one nucleolus; 2, cell with one nucleus and two nucleoli; 3-8, cells with two to eight nuclei; 9, cluster of nuclei that have lost the original common cell wall.

*Fig. 11.* Portion of intra-ventricular lobe of *Hylocichla swainsoni*.

*Fig. 12.* Portion of basi-occipital lobe of *Hylocichla swainsoni*.

*Fig. 13.* Magnified portion of the corpus callosum of *Hylocichla swainsoni*.

Figs. 1-4 and 10-12 are drawn to the same scale.

Figs. 6-8 are drawn to a common scale.

The outlines of all drawings of sections were made with the camera.

## EDITORIAL.

### THE PROBLEMS OF COMPARATIVE NEUROLOGY.

It is natural for workers in every department of science to feel that their own chosen field of investigation is that which opens the most direct avenue to the Arcana of nature. It is well, therefore, to reflect at times upon the necessary limitations of each sphere, as well as the connections between allied departments. The brief review here following is intended to illustrate a few recent tendencies rather than to summarize the results in all directions. Such reviews will be offered from time to time in the hope of affording a perspective of the field represented by this periodical. The nervous system, in a sense, occupies a unique position among the organs of the body, in that it is at once the medium of communication between all organs and the "governor" which adjusts the function of each several organ to every other function. Just what part the nervous system plays in creating the organs cannot be decided at present, but the phenomena of metamorphosis and of trophic action indicate that the initiative in many cases proceeds from the nervous system. The broad generalization of modern biology that the function precedes, and, in a sense, creates its organ, when applied to the problem of animal morphology leads to the belief that in tracing the evolution of the nervous system we are to a very considerable extent determining the progressive revelation of that which differentiates the animal from the inanimate residuum.



The problems of neurology resolve themselves into the purely structural investigation, which appeals to microscope and microtome, and physiological questions involving a knowledge of the behavior of the living cell under the most diverse conditions, as well as of the laws of composition of function due to their interaction. Yet a higher class of problems, which properly transcend the sphere of neurology, as of all purely observational science, respecting the relation of body and mind, can never be wholly ignored.

In the study of all these questions the methods and results of morphology must always guide the investigator, though it is not less true that the solution of many of the vexed riddles of morphology depends upon the recognition and employment of neurological laws and generalizations. That part of the field which is being cultivated with the most zeal and success is the structural province. Yet in this most promising department the accumulation of details has too often proven unfruitful for the lack of a sufficiently comprehensive view of the entire field to enable the investigator to appreciate the bearings of isolated facts.

The objection once urged against the employment of comparative data in the determination of the functions of the human organs, *i.e.*, that there can be no proof of homology between the brain of man and that of lower animals has been removed by the researches of Keen, Lloyd, Nancrede and Horsley, which prove the substantial similarity in function of the various cortical areas in man and the higher apes.

The brilliant success which even now attends operations for the removal of localized cerebral disturbances based on the data derived from experiments upon lower animals is practical demonstration of the utility of the science, but in the light of what has been done the future is palpitant with suggestion.

During the last few years the more general homologies have been established within the group of vertebrates, and such papers as that of Alborn on *Petromyzon* have laid the

foundation for the analytic study of the brain from the comparative standpoint.

It has so often happened that just the clue necessary for the explanation of a complicated nervous structure has been found in the simpler homologue in a lower type, that it seems strange that the comparative method has been so frequently neglected, and especially that embryology has been so little employed in the investigation of the more complicated organs. Nevertheless, since the publication of the exhaustive work by Mihalkovics on the "Development of the Vertebrate Brain," a great deal has been contributed to our knowledge of the architectonic of the nervous system by embryology.

To a very large extent, effort has been concentrated of late upon histological investigation, and, as usual, the primary impetus has been given by improvements in technique which make accessible to any one structures which from their delicacy and minuteness had hitherto been regarded as beyond the reach of observation. These refinements in technique have also had the effect of undermining several of the most substantial generalizations of an earlier decade.

The methods which have excited most interest, and from which much is expected, if not already obtained, are the various forms of metallic impregnation introduced by Golgi, elaborated by Cajal and adopted by Kölliker. While all of these methods are more or less fickle and open to the objection that they emphasize one element in the structure without affecting the others, and do not with certainty differentiate nervous from non-nervous structures, yet in careful hands the results can but prove very suggestive. The following brief summary may serve at once to show what has been done and to indicate the paths by which greater attainment may be reached.

It is to-day an unquestioned dictum of biology that function and structure are intimately connected, and that difference in function implies difference in structure. Yet in the

case of the spinal cord it is impossible to assert that such a relation has been demonstrated. For example, we know that certain parts of the cord are the peculiar seat of sensory activity, while others form centers for motor reactions, yet it would be very difficult to point out exact anatomical distinctions characteristic of these two areas. The following is a condensed resumé of Golgi's results:<sup>(1)</sup>

1. All ganglion cells of the spinal cord (those of the dorsal cornu and Clarke's column not excepted) are provided with a special process connecting with a nerve and differing in physico-chemical peculiarities from all other processes. This process alone is a safe criterion for identifying a cell as nervous. Upon this basis alone I identified numerous ganglion cells in the substantia gelatinosa of Rolando. All the cells of the spinal cord are, therefore, from the standpoint of their specific function unipolar, the single process referred to being the *nervous process*.

2. The so-called *protoplasmic processes* of the cells are neither directly nor indirectly the source of nerve fibres, but they are closely associated with connective tissue cells and blood-vessels. They apparently constitute the avenues by which nourishment reaches these cells from blood-vessels and connective elements.

3. A comparison of the cells from various parts of the grey matter of the spinal cord reveals certain differences in the form, size, and ramifications of the protoplasmic process, yet the only important distinctions are such as relate to the nervous processes.

4. Upon this basis two sorts of cells may be recognized in the spinal cord, thus: (*a*) ganglion cells, in each of which the nervous process divides into minute fibrils, so that it loses its individuality in the formation of a diffuse nervous reticulum; (*b*) ganglion cells which give rise to an axis cylinder, though there may be small lateral processes.

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1 GOLGI. Ueber den feineren Bau des Rückenmarks; Anat. Anz., No. 15, 1890.

The cells of the first class predominate in the dorsal cornu, especially in the substantia gelatinosa of Rolando and may be regarded as sensory, while the second class predominates in the ventral root zones.

5. In the gray substance there is a diffuse nervous reticulum, which is also continued into the medulla and higher regions. This reticulum in the spinal cord consists of the following elements: (*a*) fibres partly from the reticulum of the gelatinous substance and partly from the dorsal cornu proper; (*b*) nerve fibres from the dorsal roots, which subdivide in the same complicated manner as described for the processes of the nerve cells; (*c*) fibrillæ from the processes just named, which retain their identity; (*d*) fibrillæ which arise from the axis cylinders of the various columns and pass transversely into the gray matter and there subdivide as in the other cases.

6. In order to establish the functions of cells or cell-clusters from the evidence of anatomy, one must chiefly rely upon the course and relations of the nervous processes.

7. In the gray substance of the spinal cord it is impossible to give an accurate topographical description of the groups of ganglion cells, because their distribution varies exceedingly in the smallest areas; neither would such a grouping be serviceable, for it does not appear that cells of the same group necessarily have the same function. It, in fact, frequently happens that adjacent cells send their nervous processes in opposite directions.

The following cells belong to the first class (those in which the nervous process terminates in a reticulum): (*a*) cells of the substantia gelatinosa of Rolando; (*b*) cells of the dorsal cornu proper; (*c*) sporadic cells in the zone between the dorsal and ventral and even within the latter.

To the second class (those with axis cylinder processes) belong the following: (*a*) the larger part of the cells of the ventral cornua; (*b*) a few cells pertaining to the dorsal;

(c) sporadic cells, especially in proximity to the lateral columns.

The ganglion cells of the anterior cornua usually send their processes directly or indirectly either to the ventral roots or a medullary column; a considerable number, however, may be followed through the ventral commissure to the columns of white matter of the opposite side. I have also observed cases where the cells of the ventral cornu of one side send processes through the ventral commissure to the fibres of the ventral columns of the other side. The above course is pursued by most of the fibres from a group of cells laterad to the *canalis centralis*, though some of the fibres pass to the lateral columns of the opposite side.

Those cells which occupy that part of the gray matter adjacent to the lateral column send their process, for the most part, to that column, but a part of the fibres pass to the other side.

In seeking examples of undoubted motor cells, only such as show an evident direct connection with a ventral root could be safely chosen. In these cases a remarkable peculiarity consists in the fact that their fibres, generally before entering the nerve root, give off a certain number of exceedingly delicate fibrils, which curve toward the ventral part of the gray substance and fuse with the complicated nervous reticulum existing there. "The motor cells then stand in immediate but not isolated connection with a nerve fibre."

The dorsal nerve roots consist solely of fibres whose axis cylinders enter the gray substance and there subdivide and assist in forming a diffuse reticulum.

[It should be stated that Lenhossék has showed, July, 1890, that fibres arising from cells in the lateral part of the ventral cornu pass through the dorsal roots and through the spinal ganglion without entering into connection with cells of this ganglion.<sup>(1)</sup>—C. L. H.]

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<sup>1</sup> Anatomischer Anzeiger, 1890, Nos. 13 and 14.



In summing up his results, Golgi emphasises the view that the nerve fibres within the central organ are not isolated, but give evidence of being related to a number of cells. This conception excludes that of sharply limited and localized areas governing a given function.

An important theoretical conclusion which apparently does not grow out of the discussion, Golgi expresses as follows: "Inasmuch as I am convinced that what we conventionally term soul is merely the interplay of the correlated activities of the various parts of the central nervous system, an activity which becomes more complicated (more genuinely psychical) the more highly differentiated and complex the component parts become, it not only seems to me that this distinction (between psycho-motor and psycho-sensory centres) is superfluous, but I incline to the assumption that no essential difference exists between the individual activities of the various cell-clusters in separate provinces."<sup>(1)</sup>

In the sphere of experimental physiology interest still centres largely in the localization of functions in sharply limited areas of the cortex. Against the precise and positive statements of Munk innumerable objections, mostly of a negative character, have been raised. The portion of Munk's results which has been most severely handled is his claim that it is possible to establish the existence of sharply defined cortical areas in the occipital lobe of one side corresponding to diagonally opposite areas of the retina of the opposite eye. A very direct and complete apparent substantiation of this view is afforded by the investigations of Obregia<sup>(2)</sup> who, under the guidance of Munk, conducted a series of experiments upon the motions of the eye in response to irritation of various parts of the visual sphere. Obregia carried on all of these experiments without the aid of anæsthetics, under the

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<sup>1</sup> For list of Golgi's papers see end of his summary in *Anatomischer Anzeiger*, No. 15, 1891.

<sup>2</sup> A. OBREGIA, Ueber Augenbewegungen auf Sehsphären-Reizung, *Archiv. f. Anat. und Phys.*, Jahrgang 1890; *Phys. Abth.*, p. 260.

belief that consciousness is a necessary condition to such reactions. Inasmuch as these motions are called out by irritations of various spots within the visual (sensory) area having no direct relation to the eye-muscle centre "F," as determined by Fritsch and Hitzig, and since the resulting motions are correlated just as they would be if the animal were consciously fixing the gaze upon a special point, and, finally, because these phenomena can only be prevented by division of the fibres of the corona radiata, Obregia concludes that such irritation actually produces optic sensations.

It is generally admitted that an irritation of a spot upon the retina produces in consciousness the image of an external luminous point in the diagonally opposite part of the field of vision. The experiments show that irritation of the posterior part of the visual area produces an upward motion of the eye-ball, an irritation of the anterior part, a motion in the downward direction, or, in other words, just the same motion as would be called out by the irritation of the lower or upper retinal areas respectively. The irritation of the centre of most distinct vision produces simply the appearance of attentive gazing with slight motion.

Without following these experiments in full, it may be said that, if proven accurate, they seem to verify the most detailed ascertions of Munk and prove a direct connection between the sensory and motor areas.

There can be no doubt that the theoretical problem of morphology, which has excited most interest of late and which seems to have the strongest hold on the imagination of investigators generally, is the question as to the origin of the head and its various correlated structures. One reason for this prolonged and persistent effort to solve a problem which is essentially simply a theoretical one lies in the fact, that the formation of the head is the culmination of the whole series of progressive changes which constitutes organic evolution. Whatever view may be taken of "cephalization" in its technical form, all must agree that the tendency of evolution

has been to subordinate more and more structures and functions to the purposes of the head. Moreover, it has been more or less distinctly seen that the solution of the anatomical and then the physiological problems connected with the head is essential to the completion of any systematic theory respecting the connection between body and mind. It has been felt that if the head, with its structures so obviously intended to serve as an avenue of expression for the mind, can be explained as a compound of the somewhat modified simple elements occurring in each segment of the body of a lower animal, then the mind itself might prove but the sum of all the functions represented by these several organs, though rendered never so "psychical," by reason of their complex interaction. Probably few biologists would care to commit themselves to so extreme a view as this, yet the great problem remains: what is the relation between the functions of the nervous elements and the phenomena of mind as such, or, in other words, just what has the nervous system, and especially the brain, to do with thought. The analysis of the head may of course be pursued from different standpoints. When it was seen that many of the structures of the head, such as the upper and lower jaws and the hyoid apparatus were modified visceral arches, it was but natural that the attempt should be made to apply the same analysis to the skull itself. The failure of the now celebrated vertebral theory of the skull by no means discouraged investigators from the attempt to discover the law of combination in accordance with which the region has differentiated.

The facts that much of the head lies beyond the end of the chorda, and that the nerves of special sense seem to conform to a different plan of structure and obey a peculiar law of development, have led to the separation of a primitive anterior part of the head and brain and a secondarily acquired posterior portion. The original metamerism of the head may fail to exhibit itself in the skull, partly because so many extraneous elements have been from time to time amal-

gamated with the original cartilaginous cranium. The brain may perhaps be depended on to reveal the true history of the head. Balfour suggested that the fore-brain is the unsegmented primordial encephalon of the invertebrate progenitor of higher animals. Koelliker supposes that this unsegmented portion is an outgrowth from the anterior part of the brain proper, but the hypothesis which just now enjoys most general acceptance is that of Kleinenberg and Dohrn, which regards the fore-brain as the fused ganglia of a number of primitive segments. The ingenuous theory of Gaskell will be elsewhere alluded to.

The solution of this problem of the metamerism of the head which is most simple is that of Rabl,<sup>(1)</sup> who believes that morphologically and physiogenetically there are but two divisions in the head of vertebrates; an anterior, larger, and unsegmented portion, and a smaller, segmented posterior portion. The boundary between these portions is the auditory vesicle, which, nevertheless, belongs to the anterior part. Although the mesoderm of the anterior portion may be separated into several aggregates, they have no correspondence, whether in the method of origin or relation to the cranial nerves, with the true somatomeses.

The anterior division has the following nerve pairs, the olfactory, optic, trigeminus, and acustico-facialis, the third, fourth and sixth being derivatives of the trigeminal system. The primary nerves of the posterior division are the glosso-pharyngeal and vagus dorsad and the hypoglossus ventrad. The accessory is considered a portion of the vagus. Rabl is much influenced by the fact that the trigeminus and facialis-acusticus do not spring from a continuous nervous ridge like the glosso-pharyngeal and sensory nerves generally, but distinct from it and distinct from each other.

Anton Dohrn<sup>(2)</sup> calls attention to the fact, long before

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1 C. RABL, *Morph. Jahrbuch*. xv, 2 Heft.

2 *Anatomischer Anzeiger*, 1890, p. 56.

indicated by Spencer and Marshall, and His, that, in *Selachii* at least, the dorsal nerve roots grow from the spinal ganglion into the medullary tube, and that this process does not take place till the peripheral growth of the nerve has been considerably extended. In the cranial nerves motor fibres do pass from the region of the lateral columns into the ganglion ridge at a period earlier than that of the central growth of the sensory fibres. These motor fibres find their way to the muscles of the visceral arches. These fibres are always on the inner side of the ganglion.

The ganglionic ridge originates from an outgrowth of the dorsal part of the medullary tube where the closure is effected. That portion of the ganglionic ridge which is not transformed into actual ganglia is destroyed. Dohrn suggests that the ridge is simply a primitive condition of the ganglia and that they are only apparently nonsegmented at the beginning, but wherever, as in the neck, they are not too much crowded the ganglia are obviously distinct, though connected, from the first.

In the attempt to separate the trigeminus and facialis acusticus from the vagus and glossopharyngeal, Rabl distinctly terms the hypoglossus the ventral root of the neuromere, of which the vagus is the dorsal root. Dohrn, however, quotes the observations of Balfour, Wijhe, Froriep and Ostraumoff, as well as his own, in support of the view that the hypoglossus contains all that remains of several spinal nerves. The discovery of two or three ganglia in early embryos of selachians attached to fibres of the hypoglossal and the rapid disappearance of these ganglia without the formation of sensory fibres may be regarded as strong evidence of the development of the motor roots of XII from the vagus neuromere. The trigeminus, facialis, glossopharyngeal and vagus all contribute to the formation of organs of the lateral line, while no spinal nerves sustain any such relation.

That no motor fibres enter any of the spinal ganglia, as



stated by Dohrn, seems to the writer doubtful. The other statement, that the entrance of the sensory roots of the vagus and glossopharyngeus into the medulla results in a decided segmentation of the latter, seems to have much evidence behind it, and though the acceptance of this evidence will perhaps make it necessary to regard the vagus as polymeric, yet the same reasons enforce the homology between the vagus, facial and trigeminal and the true spinal nerves.

The difficulties in the way of a satisfactory solution of the nerves of the eye-muscles increase with research. The fact that they primarily have root ganglia and the presence of a chiasm in the fourth prevent the acceptance of Rabl's theory of derivation from the trigeminus. The organs of sense cannot be divorced from the nervous system, and not the least important step in the solution of the problem of cephalic metamerism will be the determination of the locus and nature of the organs of special sense. An excellent general review of this field is given by Professor C. A. Whitman.<sup>(1)</sup> The comparison of the segmental sensory organs of annelids with the organs of special sense generally, is certainly suggestive. And while it seems to the writer that there can be no doubt that the pineal body has functioned as an eye in many cases, it does not appear that its unpaired character need at all militate against the theory that the vertebrate eye is an excessively modified descendent of a non-specialized sensory organ, like the segmental sensory organs of Vermes. That the paired visual organs are older, phylogenetically speaking, than those of either of the other special senses seems probable. May it not prove that the paired eyes were developed before the primitive nerve plate became a tube and that when the invagination of the neural epithelium did occur the germinative retinal cells were included in the involution, and that the

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<sup>1</sup> Biological Lectures delivered at the Marine Biological Laboratory of Woods' Hole, 1890, p. 27.

pineal eye was developed to function during the period of metamorphosis, during which the organ adapted itself to the new conditions?

This theory may serve to explain the different course of histogenesis pursued by the eye as compared with the other organs of special sense.

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#### TECHNIQUE AND MEMORANDA.

METHYL BLUE NERVE STAINING INTRA-VITAM.—The various methods of injecting staining reagents into the circulation depending on incipient degeneration of the tissues or the access of air to precipitate or differentiate the colors, have thus far promised more than they have fulfilled. The most promising of these, the methyl-blue stain, has received a searching analysis at the hands of Dr. B. Feist. (<sup>1</sup>) The process as introduced by Ehrlich, consists simply in injecting into the nervous system (cutaneous vein or lymph hearts in the frog) a concentrated solution in normal salt fluid. The difficulties chiefly grow out of the tendency of the color to fade rapidly after development, but these may be avoided by fixation in Hoyer's picrocarmine. When used quite dilute and for not too long a time the blue color is scarcely altered by its use while a longer action alters the color to Burgundy red, or rusty red, while the nuclei of adjacent cells are faintly tinted with rose. The exact reaction which takes place in the nerve, after vital impregnation with methyl blue and exposure to the air, is a matter of debate. Aronson says, that during life nerves are so well supplied with oxygen that the methyl blue absorbed by them cannot be reduced. After the death of the animal nearly all the colored portions, as well as the nerves, are rendered colorless, because the affinity of the protoplasm for oxygen increases to such an extent that the oxygen is abstracted and

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1 Arch. f. Anat. u. Phys. 1890. Phys. Abth. p. 116.

the methyl compound is reduced to leucomethyl blue, which is colorless. Nevertheless as soon as these tissues are exposed to air in thin layers, the oxidation is repeated and the color reappears.

Feist considers it improbable that oxidation alone is sufficient to explain the change, and cites many careful experiments to prove that the phenomena are connected with decomposition.

For sections, fixation of the stained tissue with platinic chloride proved useful, though the color became granular after such treatment. For nerves, treatment with Hoyer's picrocarmine for fifteen minutes, and then with osmic acid for a similar time, was sufficient to prepare them for imbedding in gum arabic and glycerine. Three or four days may be necessary before the mass becomes of a suitable consistency to cut when enclosed in pith. This method has many difficulties growing out of the brief period during which the preparation is in condition to section. The color, if fixed by osmic acid, is not permanent.

For the interesting results of the application of this method, as well as a comprehensive review of the literature of nerve histology, the original paper should be consulted. The following papers will also be found useful;

*O. Schultz.* Die vitale Methylenblu reaction der Zellgranula. *Anatom. Anzeiger*, 1887, No. 22.

*P. Ehrlich.* Ueber die Methylenblaureaction der lebender Nervensubstanz. *Deutsch Med. Wochenschrift*. 1886, No. 4.

*C. Arnstein.* Die Methylblaufaerbung als histologische Methode, *Anat. Anz.* 1887, No. 17.

*H. Kuchn.* Notiz u. vitale Reaction der Zellgranula nach subcutaner Methylblauinjection. *Arch. f. Anat. u. Phys.* 1890.

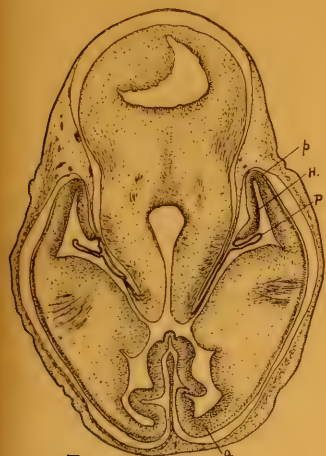


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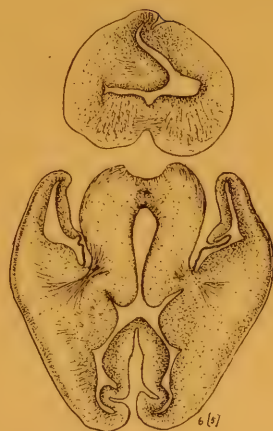


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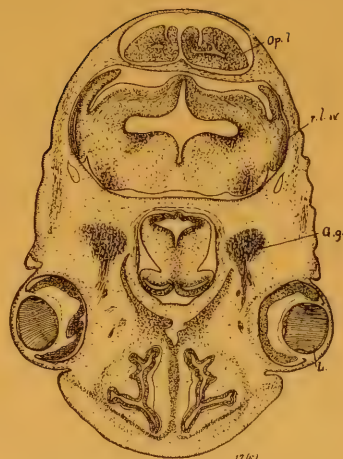


Fig. 3.



Fig. 4.



Fig. 9.

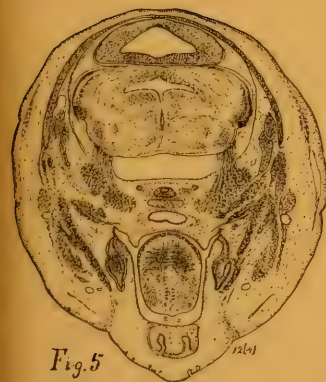


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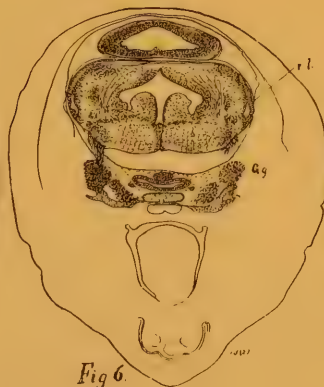


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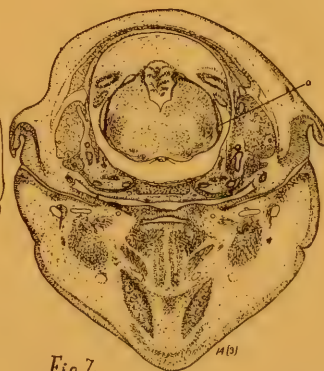


Fig. 7.



Fig. 8.

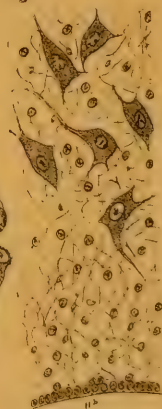


Fig. 10.





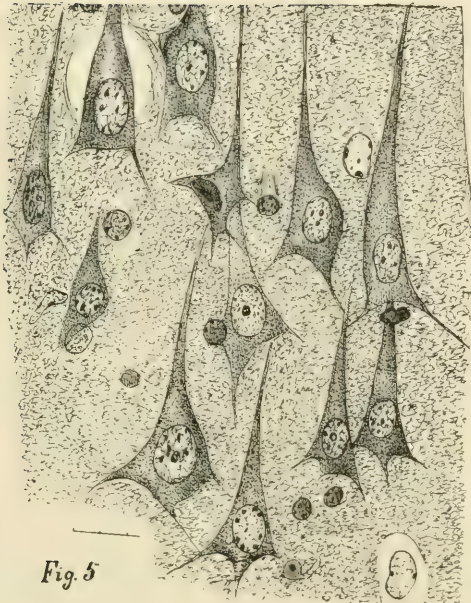
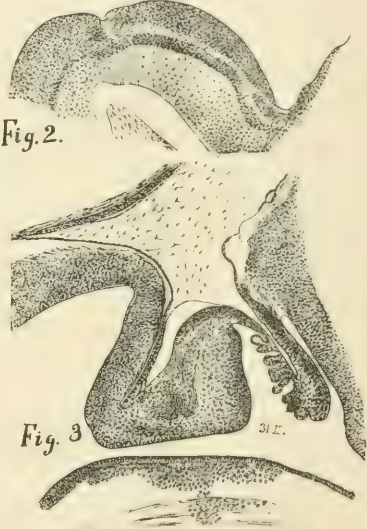
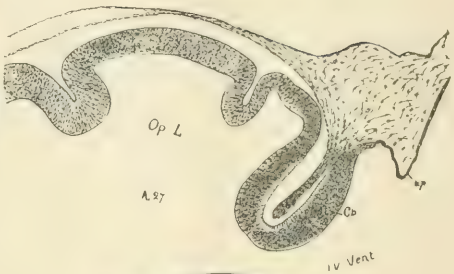
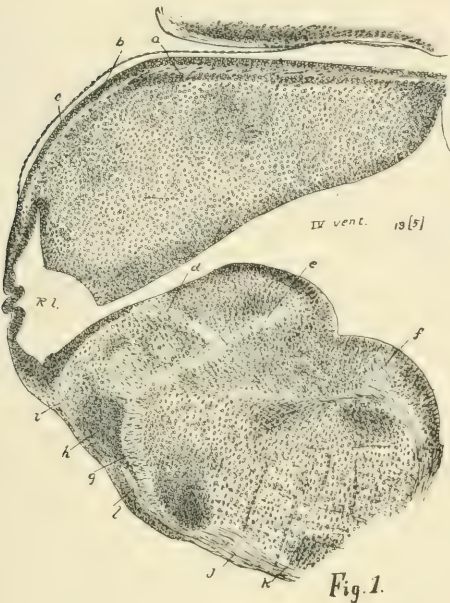






Fig. 9



Fig. 10.



Fig. 11.



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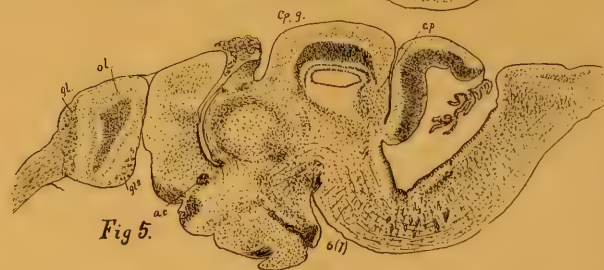


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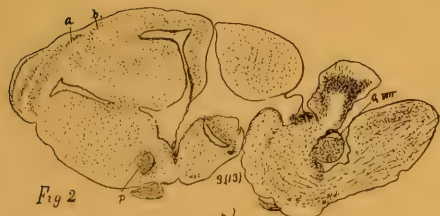


Fig. 2

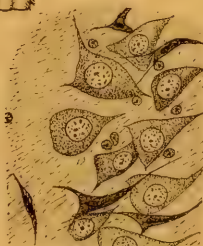


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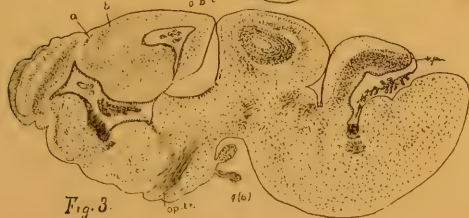


Fig. 3



Fig. 6.



Fig. 7.





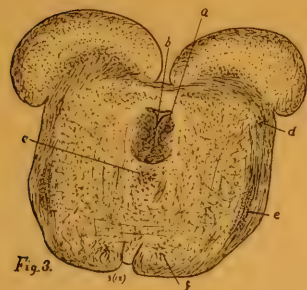


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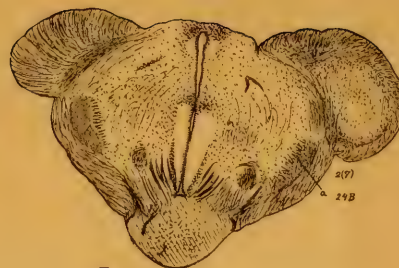


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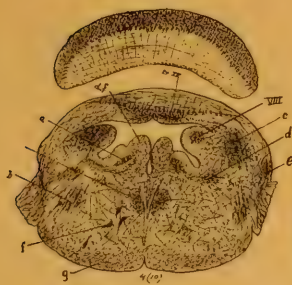


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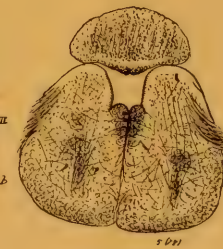


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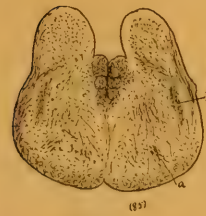


Fig. 11.



Fig. 12.



Fig. 13.

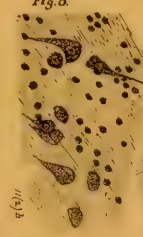


Fig. 14.



Fig. 15.



Fig. 16.







Fig. 1

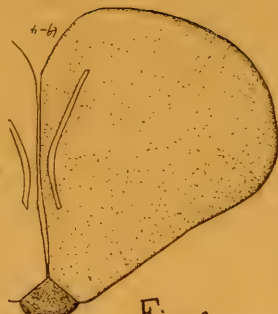


Fig. 2

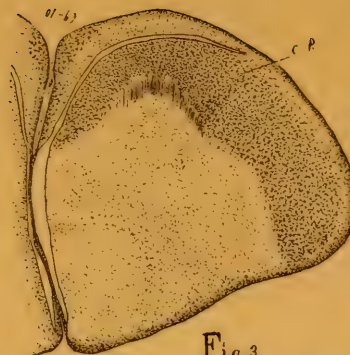


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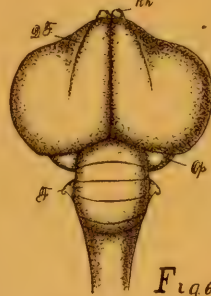


Fig. 6



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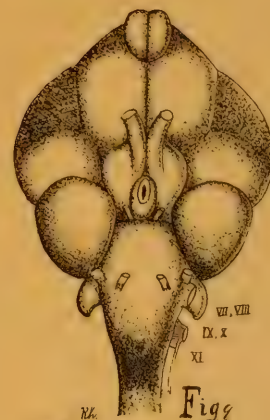


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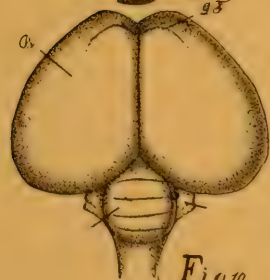


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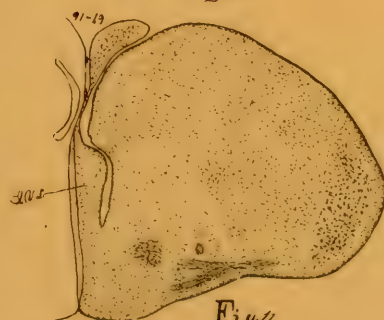


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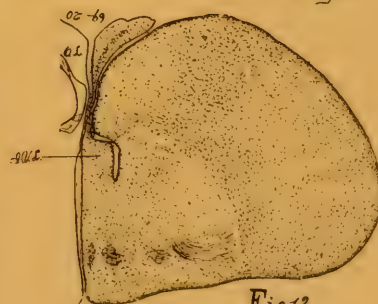


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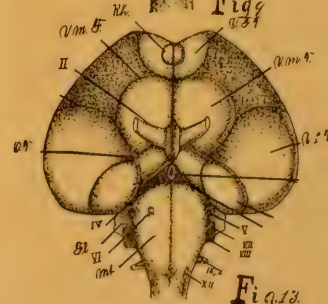


Fig. 13



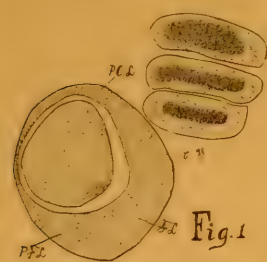


Fig. 1

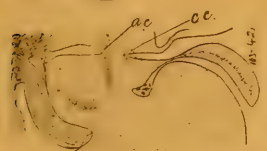


Fig. 2



Fig. 3



Fig. 4



Fig. 5



Fig. 6



Fig. 7



Fig. 8

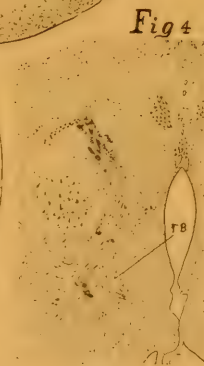


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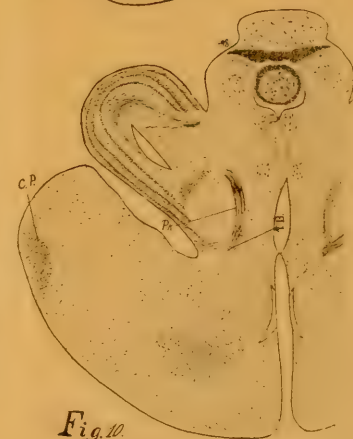


Fig. 10





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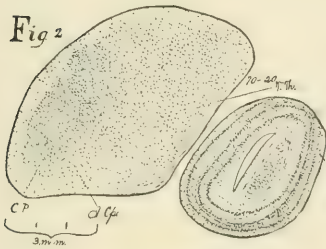


Fig 3

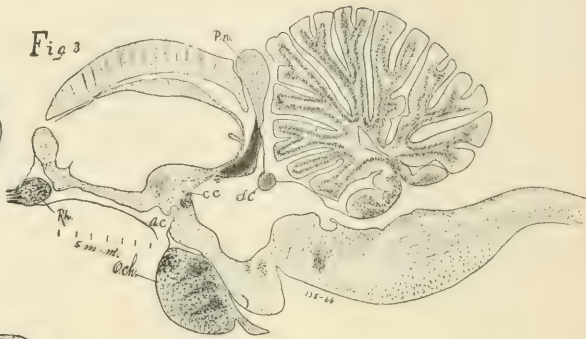


Fig 4

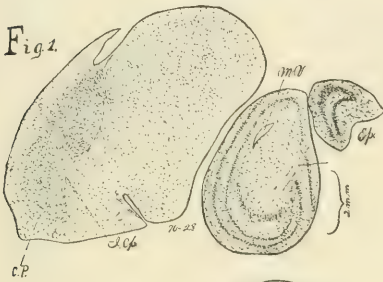


Fig 5

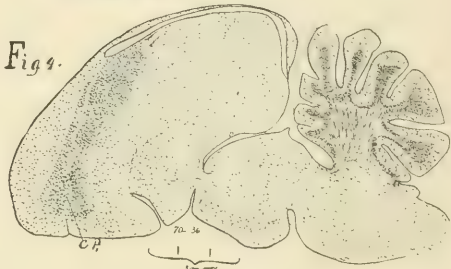


Fig 6

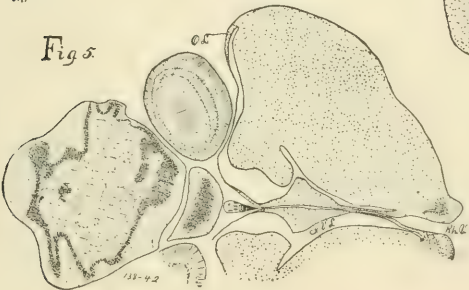


Fig 6

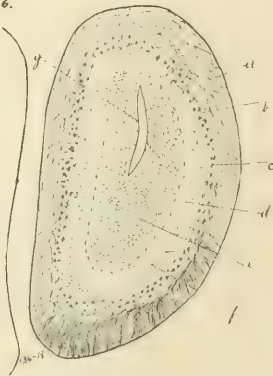


Fig 7



Fig 8

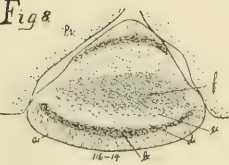


Fig 9



Fig 10

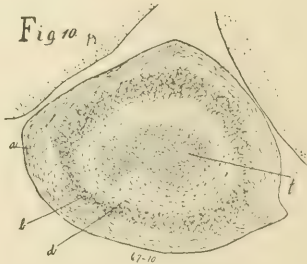






Fig. 1

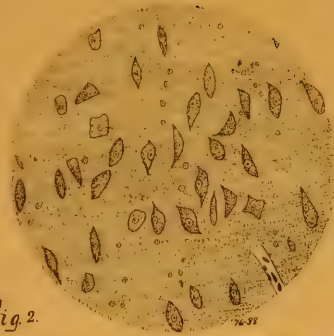


Fig. 2

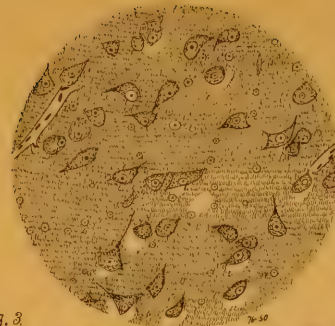


Fig. 3



Fig. 4

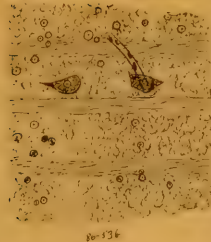


Fig. 5

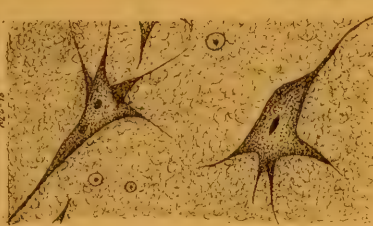


Fig. 6

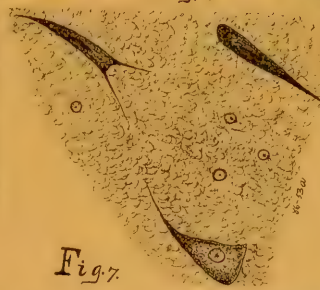


Fig. 7

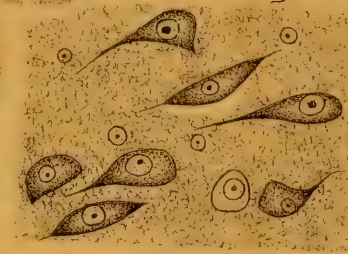


Fig. 8

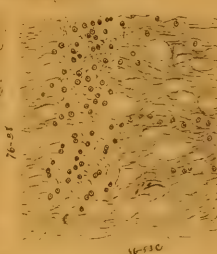


Fig. 9



Fig. 10



Fig. 11

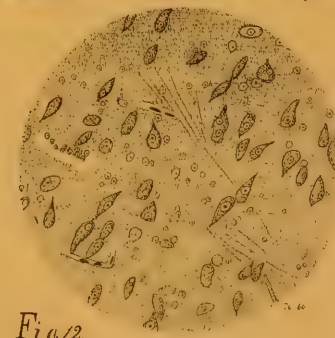


Fig. 12



Fig. 13





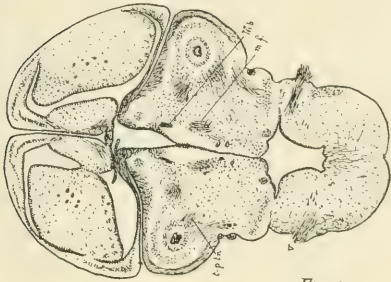


Fig. 5.

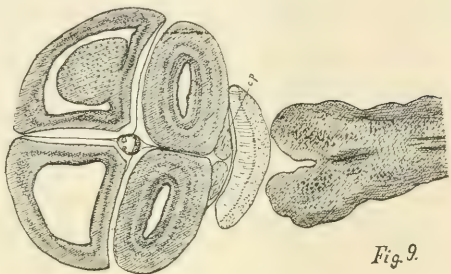


Fig. 9.

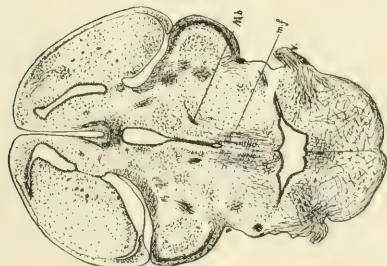


Fig. 4.

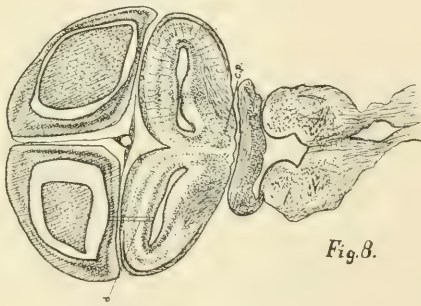


Fig. 8.

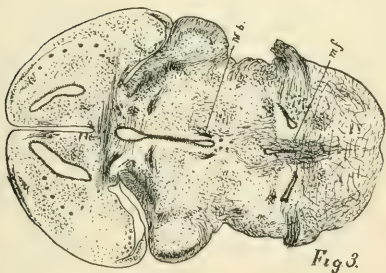


Fig. 3.

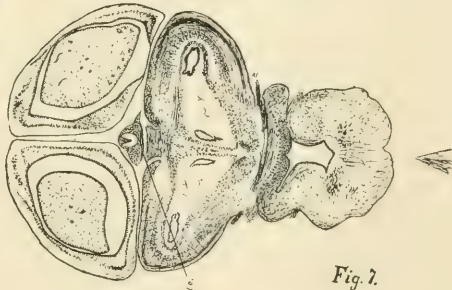


Fig. 7.

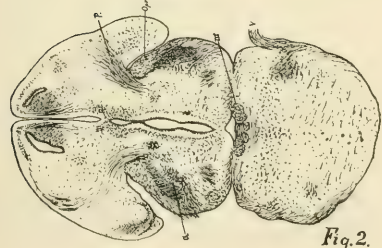


Fig. 2.

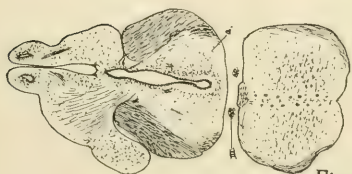


Fig. 1.

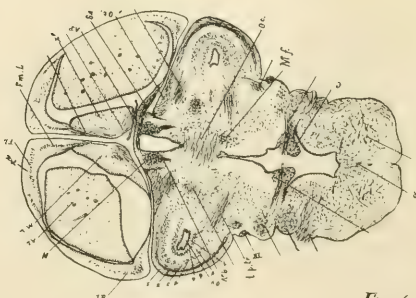


Fig. 6.





## MORPHOLOGY OF THE AVIAN BRAIN.

( *Continued.* )

C. H. TURNER.

*Additional Remarks upon the Corpus Callosum.*—Since the publication of the first paper of this series, my attention has been called to Professor Osborn's paper upon "The Origin of the Corpus Callosum, a Contribution upon the Cerebral Commissures of the Vertebrates."<sup>(1)</sup> In that paper the author makes the following instructive remarks:

"If the brain of a duck (*Anas boschas*) be carefully removed from the skull and the membranes uniting the hemispheres cut, these bodies may be gently separated until the anterior commissure comes into view; immediately above and behind this is a fine white strand of fibres, quite as figured by Meckel (1816), and so distinct that one cannot understand how it was overlooked by Stieda. This little bundle, which represents the rudimentary corpus callosum, forms a portion of the lamina terminalis, and is about one-sixth the diameter of the anterior commissure. It lies some distance below the foramen of Monro, and in vertical as well as transverse sections its fibres are seen to pass directly upwards in the thin inner wall of the lateral ventricle. So far as could be ascertained, none of its fibres pass back into the hippocampal region, as the commissure of the cornu ammonis."

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1 Morphologischer Jahrbücher, Bd. xii, pp. 223-251, 530-543.

It affords me pleasure to state that my observations upon this commissure substantiate and extend those of Meckel and Professor Osborn. My sections show a corpus callosum, not only in the brains of the lower type of birds, but also in the encephala of the highly-specialized Passerine group. Therefore, I think we may safely emphasize the statement that all birds have a corpus callosum.<sup>(1)</sup>

*Errata.*—Before proceeding, I would like to correct a couple of misprints that crept, unobserved, into the first paper of this series. The first occurs on page 57, seventh to ninth lines. Those lines should read: "The waders and fowls and their affines are placed in group 'B.' The remainder of the carinate birds fall in group 'A.'" The second error occurs on page 91. The last statement in the explanation of Figure 3 of Plate VII should read: "S. C., posterior commissure."

*Technique.*—Additional remarks upon the methods employed may seem superfluous. It must be remembered, however, that different tissues require different treatment. In the prosencephalon, where tracts are few and quite distinct, a stain that differentiates cells well, even though it does not dye the fibres, is all-sufficient. In the diencephalon and mesencephalon, however, where fibre tracts are numerous and somewhat intermingled, it becomes imperative to use a stain that differentiates fibres. While looking about for a good fibre stain, Kölliker's article, "Zur feineren Anatomie des central Nervensystem,"<sup>(2)</sup> was referred to. The plates illustrating that article are excellent. In them the finest nerve fibres are depicted. The sections from which these remarkable plates were drawn had been prepared by Golgi's shorter method,<sup>(3)</sup> and I determined to test the application of the method to avian brains. The brain of a pigeon (*Columba livia*) was selected for the experiment.

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1 JOURNAL OF COMPARATIVE NEUROLOGY, Vol. I, p. 76.

2 Zeit. f. wiss. Zool., Bd. LI, taf. i-vi.

3 Op. cit., Bd. LI, p. 9.

The encephalon was removed and the lateral half of one optic lobe and all of the prosencephalon and epencephalon dissected away. What remained was immersed for one hour in a 2 per cent. aqueous solution of potassium bichromate. It was then placed in a 3 per cent. solution of the same substance. After remaining in this fluid for twenty-three hours, the specimen was transferred to a mixture of three parts of a 3 per cent. aqueous solution of potassium bichromate and one part of a 1 per cent. aqueous solution of osmic acid. After remaining in this medium for twenty-five hours, the specimen was washed in a .75 per cent. aqueous solution of silver nitrate, and then immersed in a 1 per cent. solution of the same salt. There, protected from the light, it remained eight days. The brain was then transferred to 50 per cent. alcohol, after which it was hardened and sectioned in the usual manner. Although every precaution was taken to insure success, yet the desired result was not produced; it was impossible for me to decide what had been impregnated, for evidently much was stained that was not nervous, and it was equally evident that not all nerve tracts had been acted upon by the reagent. While still seeking a good fibre stain, I tried overstaining with Professor Herrick's modification of Grenacher's hæmatoxylin.<sup>(1)</sup> The result was quite satisfactory. The fibers were well differentiated, and the nerve cells, although stained quite densely, were not destroyed.

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#### IV.—HISTOLOGY OF THE DIENCEPHALON AND MESENCEPHALON.

*Third ventricle* (Plate VII, Figs. 3, 7; Plate XIV, Figs. 11, 13; Plate XV, Figs. 4, 5, 6, 7, 8).—In birds the diencephalon is small but compact. The third ventricle is the only cavity within it, and is very narrow. This ventricle

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<sup>1</sup> This consists of Grenacher's hæmatoxylin to which has been added a trace of corrosive sublimate. This stain cannot be used for staining *in toto*.

consists of a narrow triangular slit extending along the meson. The apex of this triangle terminates, upon the base of the brain, in the infundibulum. Caudad, this ventricle is connected with the aqueduct of Sylvius, while cephalad it is connected, through the foramen of Monro, with the lateral ventricles. It may be noted that the narrowness of the third ventricle in the avian diencephalon corresponds to the appearance of that cavity in the human brain, where, according to Ranney,<sup>(1)</sup> the third ventricle is "a narrow chink between the optic thalami."

#### NIDULI OF THE DIENCEPHALON.

*Corpus geniculatum externum* (Plate XV, Figs. 5, 7, 9, 10, 11).—Upon passing from the avian prosencephalon into the diencephalon, one of the first niduli encountered is the corpus geniculatum externum. This is a large sub-ellipsoidal cell cluster, which is situated in the cephalo-laterad portion of the dorsal region of the diencephalon. Although located at some distance from the meson, yet this nidulus does not lie adjacent to the lateral surface of the thalamus; indeed, between it and the surface there is a large fibre tract. I have already stated that this nidulus is sub-ellipsoidal. The major axis of this sub-ellipsoid is oblique to the longitudinal axis of the brain. The size of the corpus geniculatum externum varies in different bird brains. In the brain of Swainson's thrush (*Hylocichla swainsoni*) the major axis is about 1,250 micro-millimetres and the horizontal about 938 micro-millimetres long.

*Histology.*—The structure of this nidulus is unique. For the most part, the cells are arranged in irregular concentric laminae. It looks very much as though, originally, the cells had been arranged in concentric spheres, and that, by rapid growth, these spheres had become contorted.

The cells of this nidulus are fusiform (Plate XVI, Fig. 5).

<sup>1</sup> "The Applied Anatomy of the Nervous System," by Ambrose L. Ranney. Second edition, p. 312.



In hæmatoxylin and in aluminium-sulphate cochineal preparations, each cell has a faintly stained spherical nucleus and a densely stained nucleolus. In different avian brains the dimensions of these cells vary. In the thrushes (*Hylocichla swainsoni*, *Turdus migratorius*, *Sialia sialis*) these are from twenty-one to twenty-four micro-millimetres long and from seven to nine micro-millimetres broad. In addition to these large cells, the nidulus is well supplied with Deiter's corpuscles.

Bellonci has called this body the corpus geniculatum.<sup>(1)</sup> Since in the human brain we find two geniculate bodies, it is but just that some reason should be given for considering this nidulus the homologue of the corpus geniculatum externum. Ranney<sup>(2)</sup> describes the geniculate bodies of the human brain as follows:

"In the *external geniculate* body the gray matter is arranged in laminæ, which present, in cross sections made through its substance, a zigzag outline, as if the laminæ had been crushed or folded together. The cells of this nidulus are large, granular and pigmented.

"The *internal geniculate* body is less intimately connected with the optic lobes and the fibres of the optic tract, as proved by the latest researches of Flechsig, Gudden and Ganzer. *Its gray matter is not arranged in the manner peculiar to its companion*, although it is apparently traversed by the optic tract connected with both the nates and testes cerebri."

Therefore, since the above described contorted stratification is peculiar to the corpus geniculatum externum, and since the nidulus under consideration possesses that structure, the evidence that that nidulus is the homologue of the mammalian corpus geniculatum externum seems conclusive.

A large number of nerve fibres pass around the corpus

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1 "Ueber die centrale Endigung des nervus Opticus bei den Vertebraten." Von Professor Josef Bellonci in Bologna. Zeit. f. wiss. Zool., Bd. XLVII, s. 16, Fig. iii, cgt.

2 Op. cit., p. 214.

geniculatum externus; a few arise from it, and others terminate in its substance. These fasciculi will be described in connection with the tracts of the optic nerve.

*Nidulus posterius* (Plate XV, Fig. 8).—A short distance caudo-laterad of the corpus geniculatum externum, there is a small spherical cell cluster. This nidulus has been called by Bellonci<sup>(1)</sup> “nucleus posterius.” For the sake of uniformity, I have called it “nidulus posterius.” Compared with the corpus geniculatum externum, this nidulus is quite small.

Histologically, it might be considered a sphere within a sphere, the two spheres fitting so perfectly that no space is left between the inner core and the outer shell. The shell is granular, and does not contain nerve cells. The core, however, is composed of densely packed, distorted, fusiform nerve cells.

*Crescent-shaped nidulus* (Plate XV, Figs. 7-9).—In the same region, adjoining the corpus geniculatum externum and the nidulus posterius, there is a third nidulus. In horizontal longitudinal sections this nidulus is a crescent, the horns of which are directed cephalo-mesad. It lies caudad to the corpus geniculatum externum, and extends from the nidulus posterius caudo-mesad half way to the meson. Although larger than the last-mentioned nidulus, it is not so large as the corpus geniculatum.

*Histology*.—The cells of this nidulus are of two sorts, fusiform and pyramidal (Plate XVI, Fig. 3). In aluminium-sulphate cochineal and in hæmatoxylin preparations, each cell has a densely stained nucleus and a more densely stained nucleolus. The cells are closely packed, and have their major axes parallel to the longest axis of the nidulus. In different bird brains the size of these cells varies. In Swainson's thrush (*Hylocichla swainsoni*) they are from sixteen to twenty-two micro-millimetres long and from six to eight micro-millimetres wide. This cell cluster appears

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1 Op. cit., p. 16, Fig. iii; Plate V, Fig. ii, np.

to contain less than the average number of Deiter's corpuscles.

As far as I know, this nidulus has not been described before. I have ventured to christen it the crescent-shaped nidulus.

*Central nidulus of the diencephalon* (Plate XIV, Fig. 5).—In the ventral region of the brain, near the laterad portion of the diencephalon, there is a large, conspicuous nidulus. It lies upon the border of the mesencephalon and the diencephalon, and is situated about half way between the chiasm and the caudad surface of the thalamus. This is a large nidulus. It is almost as large as the corpus geniculatum externum. It is composed of fusiform nerve cells, and is traversed by medullated nerve fibres.

#### NIDULI OF THE MESENCEPHALON.

*Nidulus of the third nerve.*—In man, according to Ranney,<sup>(1)</sup> “the *motor-oculi* and *trochlear* nerves have their deep origin apparently from a gray nucleus (which, according to some authors, is common to both nerves) within the gray matter surrounding the aqueduct of Sylvius. . . . The nucleus of the fourth nerve seems to be composed of larger cells than that of the third nerve, however, and to occupy the level defined by the line of separation between the anterior and posterior corpora quadrigemina.”

From the above quotation it appears that, even in mammals, evidence is forthcoming to indicate that the niduli of the third and fourth nerves are probably distinct. In the avian brain this separation becomes more complete. These niduli are not only distinct, but they are separated by a broad longitudinal tract of nerve fibres (Plate XIV, Fig. 12). These two niduli lie near the meson in the caudo-dorsal portion of the mesencephalon, the third lying a short distance cephalo-ventrad of the fourth. The motor-oculi nidulus is a

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1 Op. cit., p. 336.

large, dense cell cluster, and is composed of irregular pyramidal cells (Plate XVI, Fig. 14). In all my preparations these cells are obscurely stained, and have dense, indistinct nuclei.

*Peduncular nidulus* (Plate XVI, Fig. 3; Plate XV, Fig. 7).—Laterad to the tract of the third nerve and about half way between the nidulus of that nerve and the base of the diencephalon, there is a large, conspicuous nidulus. This cell cluster has been named by Stieda the "peduncular nidulus." In the blue bird (*Sialia sialis*) this nidulus is about 577 micro-millimetres long and about 388 micro-millimetres wide. The most important elements of this nidulus are large, gibbous, pyramidal cells (Plate XVI, Fig. 9). In different birds the dimensions of these cells vary. In Swainson's thrush (*Hylocichla swainsoni*) they are about twenty-five micro-millimetres long and about twelve micro-millimetres wide. In the blue bird (*Sialia sialis*) these cells are about sixteen micro-millimetres long and ten micro-millimetres wide. When stained with hæmatoxylin or aluminium-sulphate cochineal, each of these cells presents a densely stained nucleus and more densely colored nucleolus.

The most conspicuous cells of this cluster are of the above type. But, in addition to these, there are a few cells of a smaller type. In Swainson's thrush (*Hylocichla swainsoni*) these cells are about fifteen micro-millimetres long and six broad, or only about half as large as the typical cells of this cluster (Plate XVI, Fig. 9). When stained with hæmatoxylin or aluminium-sulphate cochineal, these cells present small, densely stained nuclei and denser nucleoli. Although these cells appear to be pyramidal, yet they are so much smaller than the typical cells of this nidulus that one is inclined to believe that they are physiologically distinct. But the fact that these cells are not universally present in this nidulus, and that diminutive cells are often found in other niduli, gives weight to the idea that these are immature

growths of the same type as the predominant cells. In addition to these undoubted nerve cells, the nidulus contains a large number of Deiter's corpuscles. A commissure connects this nidulus with its fellow.

*Nidulus of the fourth nerve* (Plate XIV, Fig. 12; Plate XV, Fig. 5).—As has been mentioned above, this cell cluster lies near the meson in the caudo-dorsad portion of the mesencephalon. Unlike the nidulus of the third nerve, it is located near the surface. Histologically, it resembles the nidulus of the motor-oculi nerve.

In birds, as in reptiles and lower vertebrates, each optic lobe contains a ventricle. In the aves, this ventricle is a narrow expansion, which passes from the third ventricle into the body of the optic lobe (Plate XIV, Figs. 1-6; Plate XV, Figs. 2-5, 7-11). This cavity is convex, the convexity being directed cephalad. From the body of each optic lobe a dome-shaped expansion of the mesencephalon projects cephalad into the ventricle. This expansion has been called the "colliculus" (Plate XV, Figs. 2, 4). In some bird brains this feature is more pronounced than in others.

The histology of the mesencephalon is very pretty. Each optic lobe may be said to consist of an interior core or body, which is surrounded on all sides except the mesad by a stratified shell. This shell, the tectum opticum, consists chiefly of alternate layers of neuroglia and Deiter's corpuscles; while the core consists, in the main, of nerve niduli and their concomitant fibre tracts. With one exception, all the niduli of the body of each optic lobe are situated caudad to the mesencephalic ventricle (Plate XV, Figs. 5, 7-9).

*Tectum opticum*.—The tectum, as here considered, consists of all that portion of the optic lobe which lies ectad to the fasciculus internus.<sup>(1)</sup> Passing from the periphery entad through the tectum opticum of Swainson's thrush (*Hylo-*

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1 For a description of this tract see p. 129.



*cichla swainsoni*), we meet in succession the following parts (Plate XVI, Figs. 2, 12):

1. The narrow pia mater.
2. A wide layer of fibres, the external optic tracts.
3. A narrow layer of densely packed Deiter's corpuscles.
4. A wide granular layer, which contains no nerve cells and only a few scattered Deiter's corpuscles.
5. A wide layer of densely packed Deiter's corpuscles.
6. A wide granular layer which contains no nerve cells and only a few scattered Deiter's corpuscles.
7. A very narrow layer of closely packed Deiter's corpuscles.
8. A narrow granular layer which contains no nerve cells and only a few scattered Deiter's corpuscles.
9. A wide layer of densely packed Deiter's corpuscles.
10. A narrow granular layer which contains no cells and only a few scattered Deiter's corpuscles.
11. A wide layer of densely packed Deiter's corpuscles.
12. A narrow granular layer which contains no nerve cells, but numerous scattered Deiter's corpuscles.
13. An elongated nidulus, probably the *specific optic nidulus*. This nidulus consists of several longitudinal layers of elongated, slender, pyramidal cells<sup>(1)</sup> (Plate XVI, Fig. 6). The major axes of these cells are arranged approximately parallel to the axis of the nidulus. These cells are exceedingly slender, being often six to eight times as long as broad. In Swainson's thrush (*Hylocichla swainsoni*) they are from twenty-five to thirty micro-millimetres long and from three to five micro-millimetres wide. In aluminium-sulphate cochineal and in hæmatoxylin preparations, these cells are densely stained and possess dense nuclei. In addition to the cells just described, this nidulus is well supplied with Deiter's corpuscles.

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<sup>1</sup> STIEDA thinks the cells of this nidulus are fusiform. "Studien über das centrale Nervensystem der Vögel und Säugethiere." Von Dr. Ludwig Stieda, Leipzig, 1868, p. 41.

This description gives the appearance of the tectum in the caudad portion of either optic lobe. In the cephalad portion of each lobe, stratum twelve is much wider, and the cells of thirteen have become intermingled with the fibres that lie entad to the nidulus (Plate XVI, Fig. 2). Further, in the caudad portion of each optic lobe the fibre tract that forms the entad boundary of this nidulus lies immediately ectad to two large niduli, while in the cephalad portion of the same lobe that tract lies immediately ectad to the epithelium of the mesencephalic ventricle. It may be of interest to note that, in the specimens examined, this epithelium is represented by two or more rows of densely packed nuclei.<sup>(1)</sup>

To recapitulate, in general, the avian tectum opticum consists of three parts:

1. Four dense concentric shells of Deiter's corpuscles.
2. These are isolated from each other and from the remainder of the tectum by five cell-less neuroglia layers.
3. A nidulus of elongated cells. The general trend of this nidulus is parallel to the concentric shells.

I have been agreeably surprised to find that this arrangement appears to be constant. Two apparent exceptions have been noticed. In one case there were only three concentric shells, and in another there was none. However, in each of these cases it is probable that the specimens were in a pathological condition, for in one case the brain had been used in an extirpation experiment, while in the other the head containing the brain spent a mid-winter's night upon the floor of a butcher's shop. If the number of these concentric shells of the avian tectum opticum be constant, they must have a special function to perform. It seems very suggestive that Deiter's corpuscles are factors of much greater importance than is usually admitted.

Above I stated that entad to the tectum and caudad to

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<sup>1</sup> This peculiarity has been noticed by STIEPA. After describing the nerve tract mentioned above, he remarks: "An diese reiht sich das Pflaster-epithel des Ventrikels, dessen Kerne allein sichtbar sind." *Op. cit.*, p. 44.

the mesencephalic ventricle, there are two prominent niduli. One of these I have called *nidulus lenticularis*, and the other *nidulus sub-pyriformis*.

*Nidulus lenticularis* (Plate XV, Figs. 5, 7-10).—This is a large lenticular nidulus, which is situated in the central part of the optic lobe. It lies caudad to the mesencephalic ventricle, and immediately entad to the fasciculus internus. The laterad extremity of this nidulus is about on a level with the laterad extremity of the mesencephalic ventricle. The major axis of this nidulus is oblique to the ventricle, the cephalo-laterad extremity of that axis being much nearer the ventricle than the caudo-mesad extremity. In different bird brains the size of this nidulus varies. In Swainson's thrush (*Hylocichla swainsoni*) the major axis of this nidulus is from 800 to 1,000 micro-millimetres long, while the minor axes are respectively about 300 micro-millimetres and 125 micro-millimetres long. In the blue bird (*Sialia sialis*) the major axis is about 916 micro-millimetres long, while the shortest axis is about 190 micro-millimetres long.

*Histology*.—The principal cells of this cluster are large and gibbous, and have their longitudinal axes parallel to the longest axis of the nidulus (Plate XVI, Fig. 7). These cells rank among the largest in the brain. In Swainson's thrush (*Hylocichla swainsoni*) these cells are from twenty-two to twenty-six micro-millimetres long and from eight to sixteen micro-millimetres broad. In the blue bird (*Sialia sialis*) the same cells are from sixteen to nineteen micro-millimetres long and from six to ten micro-millimetres wide. In shape these cells are pyramids. A prominent fibre projects from the apical process of each cell, while smaller fibres project from each of the several basal processes. When stained with hæmatoxylin or with aluminium-sulphate cochineal, the cells are densely colored, and each possesses an elongated or sub-spherical dense nucleus and a denser nucleolus.

In some of my sections the cells of this nidulus appear to be flask-shaped (Plate XVI, Fig. 11). These cells, however,

were of very nearly the same size as those just described. Moreover, in one case the lenticular nidulus of the optic lobe of one side was apparently supplied with pyramidal cells, while the corresponding nidulus of the lobe of the other side was apparently supplied with flask-shaped cells. In this case the plane of the sections was known to be laterally oblique to the base of the brain. These facts led to the supposition that the difference in the appearance of the cells was a function of the obliquity of the plane of the sections. Since it is easy to see how pyramidal cells might thus be made to appear fusiform, and since it is impossible to see how fusiform cells could ever be made to appear pyramidal it is evident that the predominant cells of this nidulus are pyramidal.

These large pyramidal nerve cells are, apparently, not the only nerve cells in this nidulus. Many of my sections exhibit numerous smaller cells (Plate XVI, Fig. 7). These cells appear to be pyramidal. They are very slender. Although about as long as the typical cells of this nidulus, yet they are often less than half as wide. Furthermore, they have no obvious basal processes. Personally, I have grave suspicions that these may be lateral sections of the larger cells. But since I have not been able to demonstrate this, and since in other niduli there are undoubted cases of cells smaller than the typical ones, I have ventured to describe these cells. Perhaps they are immature growths of the same type as the predominant cells. This nidulus is well supplied with Deiter's corpuscles.

In addition to the large bundle that lies ectad to this nidulus, two sets of nerve fibres are associated with it. The first set consists of several loose fibre bundles, which pass from the fasciculus internus meso-cephalad through the nidulus; the other is a narrow band of fibres, which lies entad to this cell cluster and separates it from the following nidulus.

*Nidulus sub-pyriformis* (Plate XV, Figs. 5, 7-10).—This

nidulus lies cephalo-mesad to the lenticular nidulus, and is separated from it by a narrow band of nerve fibres. This is the largest nidulus in either the mesencephalon or the diencephalon. It extends from the lenticular nidulus almost to the union of the mesencephalon and diencephalon. Being widest at its contact with the nidulus lenticularis, it tapers gradually from that nidulus to its extremity. In shape this cell cluster is not a perfect pear, the symmetry being destroyed by the lenticular nidulus, which rests upon the obliquely truncated caudo-laterad extremity of this nidulus.

*Histology.*—The cells of this nidulus are numerous, and are arranged parallel to its longitudinal axis. This arrangement makes the cells of the lenticular nidulus perpendicular to the cells of the pyriform nidulus. These cells bear no resemblance whatever to those of the lenticular nidulus. They are much smaller and of an entirely different type. In the blue bird (*Sialia sialis*) these cells are about ten micro-millimetres long and five micro-millimetres broad. They are fusiform in outline, thus contrasting strongly with the pyramidal cells of the neighboring nidulus. In hæmatoxylin and in aluminium-sulphate cochineal preparations, each cell is faintly stained, and presents a clear sub-spherical nucleus and a dense nucleolus (Plate XVI, Fig. 1). This cell cluster is amply supplied with Deiter's corpuscles, and is surrounded by fibre tracts.

*Corpus posterius* (Plate XV, Figs. 5, 8).—In the caudo-laterad portion of the diencephalon, at the junction of that portion of the brain and the mesencephalon, there is a small but well-defined nidulus. This cell cluster has received several names. In 1889 Dr. Perlia<sup>(1)</sup> named it the "nidulus of the median optic fasciculus" (Kern des median optic Bündle). In the previous year Bellonci<sup>(2)</sup> christened it "corpus posterius." This nidulus varies in shape from a

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1 "Ueber ein neues Opticus centrum beim Huhne." Von Dr. PERLIA. Albrecht von Graefe's Archiv f. Ophthalmologie, Bd. XXXV, taf. ii, Fig. 5.

2 Op. cit., p, 16, Fig. iii, Kep.



sub-spheroidal to a flattened sub-ellipsoidal body. When of the latter shape, its major axis is parallel to the meson. In hæmatoxylin and in aluminium-sulphate cochineal preparations, this nidulus consists of a dense, deeply stained outer shell, within which is a solid core of lighter material. Exactly what the cell structure is, I have been unable to determine. This nidulus is surrounded by fibre tracts, and one originates in it. In all probability this body is the homologue of the testis of the mammalian corpora quadrigemina.

*Nidulus inferius* (Plate XV, Fig. 6).—Near the ventral surface of the mesencephalon, mesad to the external optic tracts and adjoining the tuber cinerium, there is an elongated lenticular nidulus. This nidulus extends from the junction of the mesencephalon with the metencephalon cephalo-mesad about half way to the optic chiasm. It is a dense nidulus, containing scattered bipolar and multipolar nerve cells. These cells are large and irregular. In hæmatoxylin and in aluminium-sulphate cochineal preparations, these cells are densely stained, and each presents an elongated dense nucleus. This nidulus is associated with both the peduncular fibres and with the fibres passing to the decussatio-inferior. Bellonci<sup>(1)</sup> has called this body the “peduncular nidulus.” But, since this name has previously been applied by Stieda to the nidulus which lies immediately laterad to the tract of the third nerve, and since two niduli of the same name in the same brain can but breed confusion, the appellation “nidulus inferius” is proposed.

*Habena*.—cephalad to the epencephalon, there is a slight dome-shaped protuberance from the dorsal surface of the diencephalon. This is the habena. In the brains examined this protuberance contains an ill-defined nidulus, the nidulus of the habena.

*Mesencephalic nidulus of the fifth nerve* (Plate XV,

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<sup>1</sup> Op. cit., taf. V. Figs. 1-4, x.

Fig. 3).—In the roof of the aqueduct of Sylvius are found a number of large flask cells.<sup>(1)</sup> These cells rank among the largest in the avian brain. Although I have not been able to trace any connection between these cells and any nerve root, yet their position, their form and their size all combine in indicating that these cells constitute the mesencephalic nidulus of the fifth nerve.

#### TRACTS OF THE DIENCEPHALON AND MESENCEPHALON.

In describing the tracts of these regions of the brain, it is thought best to consider the combined diencephalon and mesencephalon as a unit. This method has one decided advantage, it facilitates an intelligent description of the tracts. In discussing these tracts I have pursued the following order. First, I have described all the obvious commissures and decussations and all the tracts that appear to be associated with them; secondly, I have described the various nerve roots and associated fibres; finally, I have described the remaining tracts of this region.

Excluding the anterior commissure, which has been described in a previous paper,<sup>(2)</sup> this region of the brain contains six well-defined commissures and decussations. Near the dorsal surface the superior, posterior and Sylvian commissures are found; further ventrad lies the medi-commissure; while near the base of the thalamus we find the inferior commissure and the "decussatio inferior."

*Superior commissure* (Plate XIV, Figs. 8, 9).—This commissure lies in the caudad extremity of the habena. In the bird brain it is very small, and might be easily overlooked. In the amphibian brain, according to Professor Osborn,<sup>(3)</sup> "the superior commissure divides into two distinct bundles, one of which descends into the inner mantle of the

<sup>1</sup> These cells have been observed by STIEDA. Op. cit., p. 44.

<sup>2</sup> JOURNAL OF COMPARATIVE NEUROLOGY, Vol. I, p. 75.

<sup>3</sup> "A Contribution to the Internal Structure of the Amphibian Brain," by Professor HENRY FAIRFIELD OSBORN, Princeton College. Journal of Morphology, Vol. II, p. 80.

hemispheres and finally disappears after bending around into the outer portion of the mantle. The second bundle descends directly along the outer wall of the thalami. These bundles are clearly seen when the commissure is well developed.

. . . . One fact militates against our considering the commissure as a purely decussational system; that is, *the bundle entering the hemispheres is much larger than that entering the thalami.*" In the avian brain it has not been possible to find more than one tract leading from the superior commissure. The *tænia thalami*, the tract leading to the prosencephalon, is present, but the other is, apparently, absent. I say apparently, for it must be kept in mind that the avian *tænia thalami* is a very small tract; hence if in the avian brain the ratio of the tract going to the prosencephalon to the tract leading to the diencephalon is the same as it is in the amphibian brain, the tract passing to the thalamus would be so minute that its discovery would be next to impossible.

*Tænia thalami.*—This tract passes from the vicinity of the superior commissure cephalo-ventrad to the *crura cerebri*. As has been stated,<sup>(1)</sup> near the meson and dorsad to the peduncular tracts these fibres enter the prosencephalon. Immediately they turn dorsad, and, if I have traced them correctly, after passing dorsad for a short distance, they turn laterad. After traversing about half the width of the hemisphere, the tract again turns dorsad. Always keeping near the caudad extremity of the hemisphere, it continues dorsad and disappears near the dorsal surface of the brain.

*Posterior commissure* (Plate XIV, Figs. 8, 9).—This commissure lies in the dorsal portion of the diencephalon at a short distance caudad to the superior commissure. Compared with the latter commissure, this fasciculus is more than ten times as large. In longitudinal-perpendicular sections the posterior commissure resembles an inverted horse-shoe.

In the amphibia, according to Professor Osborn,<sup>(2)</sup> "the

<sup>1</sup> JOURNAL OF COMPARATIVE NEUROLOGY, Vol. I, p. 76.

<sup>2</sup> Op. cit. p. 79-80.

relation of this commissure is three-fold: First, to the oculo-motor nucleus, and probably to the main sensory tract; second, to the pale ganglion behind this nucleus; third, to the tectum opticum. As it descends the fibres divide into two bundles, of which the anterior surrounds the superior processes of the ganglion cells of the oculo-motor nucleus; the connection is so close that some of these fibres seem to be actually continuous with the cells. The posterior bundle has a similar connection with the cell processes of the pale ganglion, which may, in fact, also belong to the oculo-motor nerve. None of the fibres of this commissure can be traced directly into the main (sensory) tracts adjoining these nuclei, as observed by Pawlowsky, although such a connection seems highly probable. Dorsally, the fibres in this commissure in *Rana* can be clearly followed into the peripheral white substance of the tectum opticum, as shown in horizontal sections."

In the bird brain there is a tract which might be considered the homologue of the first two tracts described above. However, it is not connected with the nidulus of the third nerve. This tract is a bundle of fibres which passes caudo-ventrad from the posterior commissure and loses itself in the substance of the diencephalon.<sup>(1)</sup> Apparently this is a true commissure of the thalamus.

In the bird brain I cannot detect any fibres passing from the posterior commissure to the tectum opticum. This fact apparently militates against our considering the avian and amphibian posterior commissures as homologous. However, since Professor Osborn does not mention a commissura Sylvii, it seems quite probable that what he has described as the posterior commissure consists of the posterior commissure proper and of the commissura Sylvii. If this surmise be

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<sup>1</sup> In the mammalian brain, according to Professor Stricker, this tract presents the same appearance. "A Manual of Histology," by Prof. S. STRICKER. . . . American trans., edited by ALBERT H. BUCK. New York: Wm. Wood & Company, 1872, p. 693, Fig. 270, Ch.

true, then the homology between the avian and amphibian posterior commissure is sufficiently close, for the commissura Sylvii is essentially a commissure of the tectum opticum.

In the avian diencephalon two other tracts appear to be associated with the posterior commissure. One of these tracts comes from the epencephalon, the other from the metencephalon.

*Tract from the epencephalon* (Plate XVI, Fig. 4).—This tract arises in the cephalad portion of the epencephalon, and passes cephalad through the valve of Vieussens into the mesencephalon. There it loses itself in the vicinity of the posterior commissure. Apparently this tract decussates in that commissure. This tract is not the anterior peduncle of the epencephalon.

*Fasciculus cuneatus* (Plate XVI, Fig. 4).—The tract that comes from the metencephalon is probably a continuation of the fasciculus cuneatus. It passes from the medulla cephalad into the optic lobes. In company with the fibres from the cerebellum, it loses itself near the posterior commissure.<sup>(1)</sup>

*Commissura Sylvii.*—From the posterior commissure almost to the origin of the fourth nerve, the aqueduct of Sylvius is occupied by a long band of commissural fibres. As long ago as 1868 Stieda recognized this band as distinct from the posterior commissure. He christened it the “commissura Sylvii.” He included under that name not only the commissural fibres, but also the large flask cells which laterad lie ventrad to them.<sup>(2)</sup> In this paper the name is

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1 In the “Applied Anatomy of the Nervous System,” p. 230, RANNEY, in describing the tracts of the valve of Vieussens, writes: “Certain longitudinal fibres may be demonstrated which can be traced into the superior vermiform process of the cerebellum. The course of these fibres is peculiar. They decussate before leaving the superior vermiform process; they then traverse the valve of Vieussens almost to the lower portion of the corpus quadrigeminum; at this point they double upon themselves, describing curves whose convexity looks upward; finally, they join the inferior lamina of the lemniscus at its posterior bundle, and pass onward with the latter, in the posterior division of the pons Varolii to the spinal cord.” This quotation seems to indicate that the two tracts described above are one, and, further, that that one is the homologue of this tract described by Ranney. In defense, I aver that my sections do not warrant such a conclusion.

2 Op. cit., p. 44.



restricted to the commissural fibres. The cells have been described elsewhere as the mesencephalic nidulus of the fifth nerve. This commissure is identical with what some authors have named the "commissure of the optic lobes." It appears to be a true commissure of the mesencephalon. The fibres composing it arise from both the entad and the ectad sides of the mesencephalic ventricle. At the meson they converge and form a conspicuous commissure.

*Inferior commissure* (Plate XV, Fig. 10).—In the ventral part of the thalamus, between the optic chiasm and the tuber cinereum, there is a well-defined commissure. This has been named by Bellonci the "inferior commissure." In well-stained sections the fibres of this commissure can be traced into the interior of the optic lobe, where they apparently intermingle with the fibres of the fasciculus internus. The majority of its fibres pass mesad to the central nidulus of the diencephalon; a few, however, pass undisturbed through that nidulus.

*Fibræ ansulatae*.—A few fibres arise in the ventral part of the diencephalon, decussate in the region of the chiasm, and then pass cephalo-dorso-laterad, through the optic chiasm, into the prosencephalon. Bellonci thinks these fibres are homologous with the fibræ ansulatae of higher brains.

*Optic chiasm* (Plate XIV, Figs. 11, 12; Plate XV, Figs. 6, 10).—In all the specimens examined the avian chiasm differs in some essential features from that of the human subject. In the human brain some of the optic fibres decussate in the chiasm and others do not.<sup>(1)</sup> In the avian brain all of the optic fibres decussate in the chiasm. There is also another difference. In the avian brain there do not appear to be any homologues of the two commissures found in the human chiasm.

*Optic tracts*.—After decussation the majority of the fibres

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<sup>1</sup> "Applied Anatomy of the Nervous System," by AMBROSE L. RANNEY, A.M., M.D. Second edition. D. Appleton & Co. Page 351, Fig. 81.

in going to the optic tracts pass caudo-laterad and spread out over the ventral and lateral surfaces of each optic lobe. Although this is a continuous sheet of fibres, yet Bellonci<sup>(1)</sup> has divided it into two portions, a cephalo-dorsal (vorderes oberes) and a caudo-ventral (unteres hinteres) portion. Thus he obtains two tracts, which are homologous to corresponding tracts found in the brains of fishes (*Teleostei*) and amphibians. The cephalo-dorsal root passes ectad of the corpus geniculatum externus (Plate XV, Fig. 7).

All of the fibres of the chiasm do not pass into this external optic tract. A few meagre bundles lose themselves in the vicinity of the third ventricle.

Intimately associated with the external optic tracts are three fasciculi which demand our attention. Two of these tracts come from the mesencephalon and one from the prosencephalon. These tracts are: the median optic fasciculus, an unnamed tract, and tractus Bummi.

*Tractus Bummi* (Plate XV, Fig. 7).—Permit me to repeat<sup>(2)</sup> that “this tract originates in either the frontal or fronto-median lobe of the prosencephalon and passes caudo-ventrad through the intra-ventricular lobe. After passing beneath the anterior commissure, the tract turns and passes ventro-latero-caudad to the crura cerebri. Penetrating the crura, it passes to the outer fibre layer of the tectum.” Beyond its union with the external fibre layer of the tectum the course of this tract becomes obscure.

A short distance caudad to the fusion of tractus Bummi with the external optic fibres, a tract from the interior of the optic lobe unites with the external optic fibres (Plate XIV, Fig. 11). This seems to indicate that Bumm's tract passes into the interior of the mesencephalon. One serious objection militates against such a conclusion, viz., the tract passing to the interior of the optic lobe has a much smaller diameter than tractus Bummi.

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<sup>1</sup> Op. cit., p. 17.

<sup>2</sup> JOURNAL OF COMPARATIVE NEUROLOGY, p. 76.

*Median optic fasciculus* (Plate XIV, Fig. 7).—This is a well-defined bundle which arises from the corpus posterior and passes to the cephalad portion of the optic lobe. There it turns laterad and fuses with the external optic tract. Throughout its entire course this tract lies ectad to the mesencephalic ventricle. In passing from its nidulus to the external optic tract this fasciculus describes an ectally convex curve.

In 1889 Dr. Perlia<sup>(1)</sup> destroyed the retina of one eye of a young chick and then allowed the specimen to live for several months. The brain was then removed and prepared for microscopical examination. As a result of the extirpation it was found that, in the optic lobe connected with the injured eye, several tracts had atrophied. One of these atrophied tracts was the one just described. This experiment seems to demonstrate that this tract is connected with the optic nerve. Dr. Perlia has christened this tract the “median optic fasciculus.”

*Third nerve* (Plate XIV, Fig. 12).—In the avian brain the root of the oculo-motor nerve is quite prominent. Arising from its nidulus in the caudo-dorsad portion of the diencephalon and passes ventro-laterad to its external root.

*Mesencephalic root of the third nerve* (Plate XIV, Fig. 3).—In addition to the main root of the third nerve, there is another tract which appears to be connected with that nerve. This tract arises in the optic lobe, entad to the mesencephalic ventricle. Describing a curve the convexity of which is directed dorsad, this tract passes mesad to the peduncular nidulus. The majority of these fibres pass through this nidulus and decussate at the meson. There are fibres which connect the two niduli, but I have not been able to trace any of these fibres into the third nerve root.<sup>(2)</sup>

1 “Ueber ein neues Opticus Centrum beim Huhne.” Von Dr. PERLIA, Augenarzt in Frankfurt a. M. Aus dem Senkenberg’schen Institute (Prof. Weigert). Albrecht von Graefe’s Archiv f. Ophthalmologie, Bd. XXXV, s. 20-24, taf. ii.

2 A tract homologous with the one just described is found in reptiles. See “Notes

*Fourth nerve* (Plate XIV, Figs. 8, 9; Plate XV, Figs. 5, 8, 9).—In the human brain, according to Ranney,<sup>(1)</sup> “the deep fibres of this nerve may be traced to four different localities, as follows: First, some to the substance of the peduncles; second, other fibres to the valve of Vieussens, where they are lost, with the exception of a few which can be traced to the frenulum; third, a few fibres to the tubercula quadrigemina; fourth, a large bundle which passes inward towards the median line and then decussate with its fellow of the opposite side.”

In the avian brain I have not been able to trace, with certainty, any fibres from the fourth nerve to the peduncles of the cerebellum. Neither have I been able to demonstrate that any of the fibres of the fourth nerve originate in the valve of Vieussens. However, homologues of the two remaining tracts are constant in the avian brain.

As in the human brain, that portion of the fourth nerve which decussates constitutes the largest root of that nerve. The fibres of the fourth nerve arise from their nidulus in the caudo-dorsal part of the diencephalon, and, after decussating in the valve, pass ventro-laterad, around the cephalad extremity of the pedunculi cerebelli, to the surface.

*Mesencephalic tract of the fourth nerve* (Plate XV, Fig. 5).—This tract arises from the fasciculus internus, at the junction of that bundle with the caudo-laterad corner of the mesencephalic ventricle. It then passes, in an undulating line, dorso-mesad to the valve of Vieussens. In all probability this tract participates in reflex actions.

From the vicinity of the niduli of the third and fourth nerves a tract passes cephalo-laterad to the prosencephalon (Plate XV, Fig. 10).

*Fasciculus internus* (Plate XV, Fig. 5).—Entad to the cell layers of the tectum opticum there is a large bundle of

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upon the Brain of the Alligator,” by C. L. HERRICK. *Journal of the Cincinnati Society of Natural History*, Vol. XII, Plate XIII, Fig. 6, R. III.

1 Op. cit., pp. 395-396.

fibres, from which several tracts arise. For this bundle the name "fasciculus internus" is proposed.

*Central tract of the diencephalon* (Plate XV, Fig. 10).—One of the most conspicuous tracts of the diencephalon is one passing from the caudad extremity of the fasciculus internus to the central nidulus of the diencephalon. Bellonci has christened this fasciculus the "central tract of the diencephalon." At one place, near the ventral surface of the mesencephalon, this tract becomes tangent to the external optic tract. At another place it is tangent to the tract passing to the inferior commissure.

Connecting the central nidulus of the diencephalon and the corpus geniculatum externus, there is a definite tract. This tract is quite short, and lies near the ventral surface of the brain. Histologically, this tract consists partly of fibres and partly of cells.

*Prosencephalic tract of the corpus geniculatum externum.*—From the cephalad (Plate XV, Fig. 11) and mesad (Plate XIV, Fig. 13) surfaces of the external geniculate body arise a number of fibres. These unite into a definite tract, which passes caudo-laterad into the prosencephalon. After entering the crura cerebri these fibres fuse with the peduncular tracts. This renders it difficult to say which portion of the cortex is supplied by this tract.

*Tract from the mesencephalon to the metencephalon* (Plate XIV, Fig. 10; Plate XV, Fig. 10).—From the caudad portion of the fasciculus internus a well-differentiated tract passes from the mesencephalon to an ellipsoidal nidulus in the metencephalon. This cell cluster lies near one of the niduli of the fifth nerve.

*Tract to the prosencephalon* (Plate XIV, Fig. 10).—Another small tract arises within the mesencephalon, and, curving around the mesad portion of the corpus geniculatum externum, passes cephalo-laterad into the prosencephalon.

*Anterior peduncle of the epencephalon* (Plate XIV, Fig. 7).—This tract passes cephalo-ventrad from the epencephalon



to the vicinity of the chiasm. It then turns cephalo-mesad and decussates in the cephalo-ventral part of the diencephalon.

*Dorso-median fasciculus* (Plate XIV, Fig. 12).—This bundle passes between the roots of the fourth and third nerves. It will be more fully described in a subsequent paper.

*Pyramidal tracts*.—In the first paper of this series all tracts, excepting the tractus Bummi, passing from the diencephalon to the prosencephalon were included under this name. Here this name is restricted to the crossed and the direct pyramidal tracts of the cord. In the lateral portion of the diencephalon these tracts pass along the ventral surface of the brain, slightly dorsad to the chiasm. Cephalad to the crura cerebri they curve laterad into the prosencephalon.

#### PLATE XIV.

*Figs. 1-6.* Transverse sections of the diencephalon and mesencephalon of *Sialia sialis*. *F. I.*, fasciculus internus; *A.*, mesencephalic tract of the third nerve; *C. P.*, corpus posterius; *N. L.*, nidulus lenticularis; *N. P.*, nidulus pyriformis; *O. C.*, commissura Sylvii; *P. C.*, posterior commissure; *P. N.*, peduncular nidulus; *S. C.*, superior commissure; *III*, root of third nerve; *IV*, root of fourth nerve.

*Figs. 7-9.* Horizontal longitudinal sections of the caudad portion of the brain of a chicken. *A. P.*, anterior peduncle of epencephalon; *D. M. F.*, dorso-median fasciculus; *M. O. T.*, median optic bundle; *O. C.*, commissura Sylvii; *P. C.*, posterior commissure; *P. N.*, peduncular nidulus; *S. C.*, superior commissure; *III*, root of third nerve; *III n.*, nidulus of third nerve; *IV*, root of fourth nerve; *IV n.*, nidulus of fourth nerve.

*Fig. 10.* Horizontal longitudinal section of a portion of the brain of *Hyllocichla swainsoni*. *A*, tract passing from the mesencephalon to a nidulus in the medulla; *IV*, root of fourth nerve.

*Fig. 11.* Horizontal longitudinal section of the diencephalon of *Columba livia*, taken near the ventral surface. *D. I.*, decussatio inferior; *F. A.*, fibræ ansulatæ; *O. C.*, optic chiasm.

*Fig. 12.* Longitudinal-perpendicular section of *Sialia sialis*, taken through the root of the third nerve. *D. M. F.*, dorso-median fasciculus; *III*, root of third nerve; *IV n.*, nidulus of third nerve.

*Fig. 13.* Horizontal longitudinal section through a portion of the

diencephalon of *Columba livia*, taken through the corpus geniculatum externum. *A*, tract passing from mesencephalon to prosencephalon; *C. G.*, corpus geniculatum externum; *C. G. T.*, tract from corpus geniculatum externum to prosencephalon; *O. C.*, commissura Sylvii.

## PLATE XV.

*Figs. 1-6.* Horizontal longitudinal sections of the diencephalon and mesencephalon of *Columba livia*. *a*, crescent-shaped nidulus; *C. G.*, corpus geniculatum externum; *C. P.*, corpus posterius; *d*, tract from within the mesencephalon to the external optic tract; *F. I.*, fasciculus internus; *g*, tract from mesencephalon to prosencephalon; *m*, mesencephalic tract of fourth nerve; *P. T.*, peduncular tracts; *N. I.*, nucleus inferius; *O. C.*, commissura Sylvii; *O. T.*, external optic tract; *T. B.*, tractus Bummi.

*Figs. 7-10.* Horizontal longitudinal sections through the diencephalon and mesencephalon of *Hylocichla swainsoni*. *a*, crescent-shaped nidulus; *b*, tract from mesencephalon to the prosencephalon; *C. G.*, corpus geniculatum externum; *C. N. T.*, central nidulus of the thalamus; *I. C.*, inferior commissure; *N. P.*, nidulus posterius; *P. N.*, peduncular nidulus; *III*, third nerve root; *III n*, nidulus of third nerve; *IV*, root of fourth nerve; *IV n*, nidulus of fourth nerve.

*Fig. 11.* Longitudinal perpendicular section of the diencephalon of a chicken. *a*, tract from corpus geniculatum externum to prosencephalon; *C. G.*, corpus geniculatum externum.

*Fig. 12.* Longitudinal perpendicular sections of the caudad portion of the brain of *Sialia sialis*. *III*, root of third nerve; *IV*, root of fourth nerve.

## PLATE XVI.

*Fig. 1.* Cells from the nidulus pyriformis of *Hylocichla swainsoni*.

*Fig. 2.* Magnified portion of the tectum of the cephalad portion of the optic lobe of *Hylocichla swainsoni*.

*Fig. 3.* Cells from the crescent-shaped nidulus of *Hylocichla swainsoni*.

*Fig. 4.* Longitudinal perpendicular section of a portion of the caudad part of the brain of a chicken.

*Fig. 5.* Cells from the corpus geniculatum externum of *Hylocichla swainsoni*.

*Fig. 6.* Cells from the optic nidulus of *Hylocichla swainsoni*.

*Fig. 7.* Cells from the nidulus lenticularis of *Hylocichla swainsoni*.

*Fig. 8.* Cells from the nidulus inferius of *Meleagris gallipavo*.

*Fig. 9.* Cells from the peduncular nidulus of *Hylocichla swainsoni*.

*Fig. 10.* Horizontal longitudinal section of part of the brain of *Columba livia*, to show the tract passing from the vicinity of the third and fourth niduli to the prosencephalon.

*Fig. 11.* Cells from the nidulus lenticularis of *Hylocichla swainsoni*.

*soni*, to show the appearance of the cells when the nidulus is cut obliquely.

*Fig. 12.* Section of tectum of the caudad portion of the optic lobe of *Hylocichla swainsoni*.

*Fig. 13.* Cells of the nidulus of the fourth nerve, from *Sialia sialis*.

*Fig. 14.* Cells of the nidulus of the third nerve, from *Sialia sialis*.

## NOTES UPON TECHNIQUE.

The following suggestions may prove useful to others as they have to us.

1. FELT-TIPPED PLIERS.—Every one has experienced the difficulty of using pliers or forceps of the ordinary pattern in handling delicate and slippery tissues. If the corrugations are sufficiently sharp to be of service there is much danger of lacerating or perforating the membrane. This is true in the dissection of amphibia with mucous glands in the skin as well as in the mucous and serous membranes of other vertebrates and the meninges of the brain. This difficulty may be almost entirely obviated by gluing to the points accurately fitted pieces of close-textured felt or chamois skin, which facilitate steady and firm tension without danger of laceration.

2. KULTSCHITZKY'S HEMATOXYLIN PROCESS.—A method which possesses many of the advantages of Weigert's, besides being shorter and more simple, is described as follows: The material is fixed in Erlicki's fluid one to two months and is then washed in flowing water one to two days. The precipitation of chromium salts, which is one of the great

drawbacks to Weigert's method, is thus avoided. The hardening takes place in alcohol as usual. After imbedding in celloidin and sectioning in the usual way, the sections are stained in hæmatoxylin dissolved in 2 per cent. acetic acid solution (100 gr. 2 per cent. acetic acid, 1 gr. hæmatoxylin in absolute alcohol). The staining may occupy one to three hours. The sections are then transferred to a mixture of one hundred parts of saturated lithium carbonate and ten parts of 1 per cent. ferrocyanide (red) of potassium. A larger amount of the ferrocyanide hastens the washing of the stain from the gray matter. The operation requires two to three hours. After washing in water the sections are imbedded in balsam as usual. The resulting preparation has the axis cylinder fibres stained dark blue or violet and the gray matter yellowish. A solution of carmine in acetic acid may be used in the same way with similar results.

3. ALUMINIUM SULPHATE COCHINEAL.—An accident led to the discovery that the substitution of aluminium sulphate for the alum called for in the formula of Czokor's alum cochineal is a vast improvement. The stain not only becomes more selective, acting almost solely upon the nuclei, but it is more prompt and reliable and the color resulting is more pronounced and agreeable. A similar substitution in other stains using alum is suggested.

## RECENT INVESTIGATIONS ON THE STRUCTURE AND RELATIONS OF THE OPTIC THALAMI.

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There has been much written of late concerning the optic thalami and their connection with neighboring structures in the brain. To present all the various views held with regard to these important basal ganglia would be tedious, while to discuss them fully within the compass of these pages would be impossible. Consequently, let us confine ourselves to the matter that has been published during and since the year 1885, filling up with discoveries made before that date such gaps as may arise, because during the last six years all structures herein brought to notice have not received equal share of attention.

A precise description of the two structures in the brains of mammals called the optic thalami, would at this stage of neurological research be unnecessary. The structure and relations of the epiphysis are not here discussed. So much has been written recently concerning this subject, that a further setting forth of it is not necessary. The reader is referred to Cattie's excellent article (*Archives de Biologie*, Tome III, 1882).

The fishes are characterized by a small development of the thalamencephalon, and in them we can recognize structures corresponding only to parts of the thalamus in the higher vertebrates, *e. g.*, that part of the thalami in the mam-



mals which is called trigonum habenulæ is found in the fishes. The thalamencephalon in the fishes seems indeed to be of small importance; it appears in many of the species as if it were a mere band of nerve-tissue, connecting the prosencephalon with the mesencephalon. In the amphibians and also in the reptiles the development of this part of the brain is carried further; not that the relative size is so much greater, but that the fibre connections are more complex. The general arrangement of the parts is more suggestive of that of the lower mammals. In the birds the thalamencephalon is perhaps as well developed as in the reptiles, but relatively to the other structures is not deemed of such importance, partly because the corpora striata are so much larger than in the preceding type, and also because of the enormous size of the optic lobes.

*Relations to Cerebral Tracts.*—We shall now consider the relation of the thalami to the basal prosencephalic tract, and at the same time, their relations to the bundles of fibres connecting them with the cerebellum, the medulla oblongata, and the optic lobes.

With regard to the teleosts, Mayser [<sup>7</sup> p. 322, et seq.] says that the connection of the valvula cerebelli with the inferior lobes is very distinct. After the tract reaches the inferior lobes, it becomes dorsal to, and spreads over the part connecting the inferior lobe and the pars peduncularis. Some of the fibres divide off, and go to the cerebellar tract. This is somewhat the same view as that of Bellonci, for he considers [<sup>4</sup> p. 24] that the inferior lobes are really parts of what he, in his researches, calls the inner and the outer commissures. Goronowitsch also states [<sup>19</sup> p. 545, et seq.] with regard to the teleosts, that the tract running through the base of the mesencephalon and ending in the region of the thalamencephalon is perhaps homologous to the tract in the subthalamic region of the higher vertebrates.

In the amphibian brain [Osborn,<sup>20</sup> p. 78] the bundle of fibres composing the dorsal portion of the cerebral

peduncles, as shown in the transverse section of the thalami, is made up of the prosencephalic sensory tracts formed by the mesencephalon and the diencephalon. The basal prosencephalic tract passes from the medulla into the basal portion of the prosencephalon. Some fibres terminate immediately below the anterior commissure, others enter the corpus striatum. He also says that the bundles of fibres coming from the lateral regions of the medulla and spreading over the mesencephalon, in the same manner spread over the diencephalon. The connection is a well-known one. As far back as 1875, Stieda [<sup>2</sup> p. 396] showed that in the case of the turtle, the fibre-bundle coming from the mesencephalon is joined by the bundle from the thalamus and continues into the prosencephalon. Stieda [<sup>2</sup> p. 395] also says that in the reptiles the nerve-fibres of the thalamencephalon are for the most part the continuations of the peduncle, both of the lateral and of the central tracts. Some fibres come from the mesencephalon, and other fibres joining these, pass to the prosencephalon; and some from the mesencephalon cannot be traced further, and probably terminate in the thalamus. This is, of course, the basal prosencephalic tract to which Stieda referred, and is exactly like the course of the fibres in the amphibian brain.

In birds, the tract in which all the fibres join, descend cephalad to the anterior commissure, to the base of the cerebrum; it passes this at the front edge of the optic tract (of the same side), goes around the crus, bending laterad, and terminates between the posterior dorsal edge of the thalamus and the optic lobe.

Edinger shows [<sup>21</sup> see Fig. 64, p. 79,] us that in the human brain the fibres passing from the anterior peduncle of the cerebellum, and running just under the corpora quadrigemina, enter the "red nucleus," after decussating, and thence send fibres to the thalamus, to the internal capsule, and to the tegmentum. The fibres passing just above the pons, go into the thalamus, and from there run dorsad in radiating

lines; some, after passing through the "red nucleus," unite with this bundle, and then go in the same direction.

*Relations to the Optic Tracts.*—Let us first consider these in the human brain. The optic nerves [Edinger<sup>21</sup>, p. 77] after crossing at the chiasma (he does not mean complete decussation) become the optic tracts; these turn around the cerebral peduncles, and passing up behind the thalami, spread out, partly entering them, but with other branches going to the cerebellum and to the nidulus of the oculomotor nerve. He thinks that some fibres that enter the thalamus, go no further, but that others do, by way of the tract towards the cortical optic centres (the occipital convolutions of the hemispheres). In the neighborhood [Stillings<sup>3</sup>, p. 474] of the optic lobes the tract divides into three branches. The first runs through and partly around the external geniculate body, and in a band thus covering the gray substance of this body, passes to the surface of the thalamus and runs on further (that is, to the cortical optic centres; see Edinger's opinion just above). The second, passing through the two geniculate bodies, and then giving off a small shoot, which loses itself in the tænia, reaches the corpora quadrigemina, where it divides into two branches, of which the one penetrates the nates, and the other, passing by on the surface and again dividing, partly forms a commissure with its fellow and partly goes to the frenulum. The third goes to the internal geniculate body, some of its fibres stopping there, but most of them, passing on, go to the nates or to the anterior cerebellar peduncles which can only partly be regarded as a branch of the opticus; its connection with the testes is certain.

Associated with the optic fibres in the teleosts [Bellonci<sup>17</sup>, p. 7] are (1) the inferior commissure, which largely corresponds with Gudden's commissure and is in connection with the inferior lobes; (2) the fibræ ansulatæ, which cross mostly above, but also partly within the inferior commissure, as in the reptiles and amphibians; (3) a small number of thick

peduncular fibres that descend from the thalamus and pass partly through the base of the optic tract, also connecting with the inferior lobes; (4) the stratum zanolæ, which does not come from the optic nerve, but from the outer layer of the anterior part of the tectum. Some fibres of the stratum zonale assist in the formation of the inferior commissure, and intertwine themselves in a complex manner with the optic and with the thalamus fibres that originate partly in the inferior commissure.

In the amphibians the optic tracts are principally confined to the median portions of the tectum opticum. According to Osborn [<sup>20</sup> p. 81, 82] they can be traced as far as the posterior portion of the lobes. A second tract arises from a mass of cells imbedded in the thalamus; a third enters the hemisphere directly. These are the main sources of origin. The course of the optic tract in reptiles, as described by Rabl-Rückard is quite similar to the course of the same tract in amphibians.

Gadow says [<sup>15</sup>, p. 378] that in the birds, the coverings of the optic lobes join on either side to form the optic tract, some of the fibres passing by the thalamencephalon and others entering it. After examining some of my own sections of the pigeon's brain, it seems to me that whatever fibres terminate in the thalamus are those coming from the chiasma; I discovered none from the corpora bigemina that terminated there. In birds, according to Bellonci [<sup>17</sup>, p. 17], the optic tract divides into two portions, an upper anterior one, and a lower posterior one. The division is not an entire separation, a layer of nerve-fibres lying between them. Of course they correspond to the optic nerve-roots of the fishes, amphibians and reptiles. The anterior one covers a swelling that no doubt corresponds to the geniculate body of the mammals. The grey substance of the thalamus is traversed by optic fibres as follows: 1. The lower ones, which, having separated from the chiasma, and being joined in small bundles, penetrate the lower grey substance of the third

ventricle; these afterwards join the main tract, mostly uniting with its dorsal anterior portion. 2. The upper ones, which pass through the geniculate body, and also join the dorsal anterior portion of the optic tract. 3. The upper fibres. These do not terminate in the thalamus, but may possibly, as in the lower vertebrates, have some connection with this grey substance through which they pass. In close proximity to the tract are peduncular fibres, other fibres that form the inferior commissure, and fibres of the subthalamic posterior decussation, corresponding, perhaps to the *fibræ ansulatæ* of the lower vertebrates. The correspondence is a true one, no doubt, for, according to Bellonci's description, and also according to the figures of the various types, the position of this decussation, as well as the terminal arrangement of the fibres composing it, are similar to those of the *fibræ ansulatæ*. There are also thick medullary fibres which, forming a network, cross inside of the inferior commissure and the decussation; and in addition to all these there is a thick bundle of medullary fibres which comes from the interior of the optic lobes and goes to the central nidulus of the thalamus.

It is Bellonci's opinion [<sup>17</sup>, p. 19] that some of the optic fibres in the mammalian brain never crosses either in the chiasma or in the subthalamic substance, and this, he says, is more easily seen in the rodents than in any other of the mammalian types. Some fibres that do not cross at the chiasma, do so in the tuber cinereum, and then join the optic tract. In the region of the chiasma the following kinds of fibres are associated with the optic ones: the inferior commissure, the inferior *fibræ ansulatæ*, of which he mentions three groups: the first goes caudad and dorsad inside of the thalamus; the second goes towards the optic tract, some of the fibres running just outside of the tract finally enter the occipital lobe; the third goes vertically dorsad and loses itself in the corona radiata, the medial thalamus fibres that pass from various portions of the thalamus to the dorsal part



of the chiasma, the lateral thalamus fibres that belong to the peduncular tract and come from the region of the interpeduncular nucleus. The optic tract, accompanied by fibres of the inferior commissure, takes a direction toward the geniculate bodies; a few leave it, but not until it has reached a position just under the internal geniculate, do the fibres of the commissure separate from the tract and enter the internal geniculate body. Most of the optic fibres remain on the surface; a few enter, but only to pass through to the surface of the thalamus. Fibres from the hemispheres, fibres from the "red nucleus," also fibres coming from the corona radiata and passing transversely through the dorsal portion of the thalamus—all these enter the internal geniculate body and by their presence render the identification of the optic tract fibres more difficult. The lower caudal root of the tract passes laterally from the geniculate body to the corpora quadrigemina. Especially worthy of notice is the connection of the thalami with the corpora quadrigemina. This corresponds to the outer anterior portion of the tectum opticum of the lower vertebrates. Near the posterior commissure this tract commences to give off branches, all of which sink into the grey substance of the nates and probably terminate there.

*Posterior Commissure.*—One probable function of this is to connect the two thalami; in fact, Mayser says [<sup>7</sup>, p. 357] that this is the only true commissure in the brain, connecting, as it does, the two sidewalls of the third ventricle. There is no such structure as the pons in the teleosts, and Rohon thinks that this posterior commissure takes its place and performs the same function as the pons of the higher vertebrates. Osborn tells us [<sup>20</sup>, p. 79] that the posterior commissure in the amphibians has a three-fold relationship: 1. To the oculo-motor nidulus, and perhaps to the main sensory tract. 2. To the pale ganglion cells behind this nucleus. 3. To the tectum opticum. As the fibres of the posterior commissure descend, they divide into two bundles; the anterior surrounds the superior processes of the ganglion

cells of the oculo-motor nidulus, the posterior connects with the cell-processes of the pale ganglion. None of the fibres of the commissure can be traced directly into the main sensory tract; in *Rana* they can be followed into the peripheral white substance of the tectum opticum. According to the investigations of Goronowitsch [<sup>19</sup>, p. 551] on the brain of *Acipenser*, the posterior commissure consists of three parts. The distal portion is formed of medullated fibres which, in sagittal sections, can be traced to the base of the mesencephalon. The proximal portion is made up of fine medullated fibres which appear to come from a group of small nerve-cells, dorsal to the bundle of Meynert; the further course of this portion he was unable to trace. The third portion is divisible into three parts: the first consists of a granular fibrous structure, in whose periphery well-defined fibres of the optic tract may be seen; the second of two or three rows of cells, the processes of which are sent out in the direction of the peripheral layer; the third is made by the inner surface of the tectum. In the proximal portion of the tectum the granular layer becomes thinner. Median to this, large, rather thickly scattered ganglion-cells are to be found. The small processes of these cells run upwards to the surface of the tectum, and appear to enter into connection with the optic fibres. Auerbach [<sup>16</sup>, p. 373 et seq.] has made a series of investigations on the structure of the posterior commissure in the teleosts and in the higher vertebrates; but the conclusions embodied in his paper need not be mentioned in addition to the above.

Pawlosky says: "The so-called posterior commissure (in mammals) consists of crossed nerve-fibres descending from the brain to the tegmentum of the crus." They originate: 1. In the habenular ganglia. 2. In the frontal lobes of the brain, through the anterior peduncle of the thalami. 3. In the temporal lobes, through the lower peduncle. 4. Perhaps in the thalami themselves.

This commissure, throughout all the vertebrate types, is

one of the first bundles to become medullated. In the human brain [Edinger <sup>21</sup> p. 73, 74] the fibres take their origin inside of the thalamencephalon near the median ganglion, and running caudad, decussate just cephalad to the corpora quadrigemina, and soon pass lower down and run along the base of the tegmentum. Running parallel to this, and being reinforced by fibres from it, they finally reach the metencephalon. The investigations of Spitzka and of Darkschewitsch confirm this statement of Edinger. The fibres that lie nearest to the median line probably terminate in the nidulus of the oculo-motor nerve.

*The Supra-commissura.*—Osborn, [“Preliminary Observations upon the Brain of Menopoma and Rana,” 1884, p. 268], says: “In the forward portion of the roof of the diacœlia (in amphibians), just above the optic chiasma, is the supra-commissura. It is closely connected with, and is just in front of the ganglia habenulæ. It passes across the posterior ends of the thalami. The distribution is similar to that of the fibres of the tænia of the thalami. It divides into two bundles, one going down to the inner mantle of the hemispheres, the other descending directly along the outer wall of the thalami. Thus it occupies the same relative position as the commissure of the pineal stalk of the mammalian brain. Osborn [<sup>20</sup> p. 80] does not consider this commissure a purely decussational system, as the bundle entering the hemisphere is much larger than that entering the thalami; consequently, it forms either partly a commissural system between the posterior portions of the hemispheres and between the thalami, or partly a decussational system between the hemispheres and the thalami. Bellonci lays especial stress upon the presence, in this commissure as in the other cerebral commissures, of decussational fibres in addition to the commissural ones. Herrick says [<sup>24</sup> p. 26]: “The supra-commissure (of reptiles) lies entirely cephalad to the habena at a level considerably ventrad to the commissure of the habena, which lies caudad to it, and passes by

a slight ventral curvature into the median part of medio-caudad projection of the cortex, and thence across to the caudo-lateral portion. The superior commissure is relatively stronger than its neighbor, and it would appear that the two are especially distinct in animals like the lizard, where the epiphysis is highly developed." A comparison of the researches in the mammalian brain with those in the brains of the lower vertebrates, would lead us to conclude that the median commissure [see <sup>21</sup> p. 63] in the one and the supra-commissure in the other, though not entirely homologous, are still in their structure and in their connections, capable of similar functions. It is Herrick's opinion [<sup>24</sup> p. 26] that instead of considering that the supra-commissura is divided into two parts in the amphibians and reptiles, we would do better to recognize two originally distinct commissures.

*Meynert's Bundle.*—Mayser [<sup>1</sup> p. 357] has told us that in the fishes this bundle consists of non-medullary fibres. It is of a single nature, running from the habenular ganglion ventrad and caudad. Breaking through the commissure of the fibræ ansulatae, it divides into many fascicles. It enlarges at the point where an addition of fibres is made from the wall of the aqueduct. Most investigators have traced the bundle only as far as the inter-peduncular ganglion, but in the amphibians Osborn has found fibres of it running past this point, and Ahlborn [<sup>10</sup> p. 285] claims that in the brain of *Petromyzon* he has traced them even into the metencephalon. Wright's investigations with *Amiurus* lead him to conclusions similar to those of Mayser just stated above. Goronowitsch [<sup>19</sup> p. 551] traced these fibres caudad only as far as the proximal boundary of the inter-peduncular ganglion. In the mammalian brain the course of Meynert's bundle is not such a simple one. The course [Honegger, <sup>23</sup> p. 407] in some of the mammals is quite different in detail from that in others. The main cause of the difference is the large development of the "red nucleus" in some of these brains. In man the bundle is very strongly deflected from its course as it passes the

“red nucleus.” In other mammals there is a slight bend, but in the mouse the course is nearly a straight line at this point. Honegger distinguishes [<sup>23</sup> p. 405] two kinds of fibres in Meynert’s bundle. The carmine stain affects one kind of fibres, making them more or less red, while the other kind remains unstained. For ventral connections of this bundle see “Interpeduncular Ganglion.”

*Infundibular Tract.*—Goronowitsch’s investigations on the brain of *Acipenser* show us [<sup>19</sup> p. 549] that the fibres in the peripheral part of the infundibular lobes run parallel to the surface. In the central portion the fibres are more definitely marked, and consist of two systems. One has its fibres parallel to the surface, as in the peripheral layer; the other crosses the first at right angles, thus having its fibres perpendicular to the surface. By means of their fibre-connections, the lobes are put into direct association with the prosencephalon. A distinct tract [<sup>19</sup> p. 550] of non-medullary fibres from the infundibular lobes passes to a ganglionic body in the wall of the mesencephalic ventricle. Osborn traces [<sup>20</sup> p. 79] the tract cephalad, in the amphibians, beneath the basal prosencephalic tract towards the hemispheres. In *Rana* it has the appearance of entering the thalami, but “not in the *Urodela*, where it appears to pass directly forwards and not upwards.”

*Mammillary Body, Corpus Candicans.*—The position of this structure just below the thalami, and its connection with the tegmental bundle, and the bundle of Vicq d’Azyr, both of which pass through or by the thalamus, bring it into notice in this article. It is particularly well developed [<sup>23</sup> p. 341] in the cat, the dog, the monkey, the rabbit, and in man. Fritsch thinks that it is homologous with the inferior lobes of the teleosts. Its main connection, as far as we are here concerned, is with the two bundles just mentioned above, but the pillar of the fornix also enters it, having, however, no functional connection with the bundle of Vicq d’Azyr, according to the careful and systematic pathological



experiments of von Gudden [<sup>16</sup> p. 429]. We must refer to Honegger's work [<sup>23</sup> p. 348 *et seq.*] for the discussion of this point. Vicq d'Azyr's bundle arises [<sup>21</sup> p. 65] from that one of the two median niduli that is caudad; it passes up through the thalamus and loses itself in the anterior tubercle. By its side, following Edinger's description [<sup>21</sup> p. 65], the tegmental bundle of the mammillary body passes dorsad, but soon separating from its companion, bends caudad, and passing through the tegmentum, can be traced to ganglia lying under the aqueduct.

*Ganglia Habenulæ* [Goronowitsch, <sup>19</sup> pp. 442, 551].—The habenular ganglia of *Acipenser* are not symmetrically developed; the right one is noticeably larger than the left. In cross-section the dorsal corner of the thalamus (into which the optic fibres run) contains the habenular ganglion. Some fibres, running into this, can be traced from the vertical rows of small cells lying between the ventricular epithelial and the granular substance. It is almost certain that these ganglia are homologues of those in the higher vertebrates, for in both types the connections with Meynert's bundle are very similar. In *Amiurus* [Wright, <sup>13</sup> p. 32] the ganglia have the same position and connections. Mayser thinks that in the *Teleosts* the bundle that passes along the upper edge of the wall of the third ventricle is homologous to the tænia of the higher vertebrates. These ganglia in the amphibians lie just behind the supra-commissura, and send out fibres forming a conspicuous tract (Meynert's) in all of these animals. Each of the ganglia habenulæ in the mammals gives off fibres which go to form Meynert's bundle. This connection is an intimate one [von Gudden, <sup>5</sup> p. 423].

*Interpeduncular Ganglion* [von Gudden, <sup>5</sup> p. 424 *et seq.*].—In the rabbit this consists of ground substance, which is an aggregation of more or less sharply defined nests of fine-fibred, band-shaped bundles, somewhat like the glomeruli of the olfactory bulb. Besides this, there are small rounded or spindle-shaped ganglionic cells. The bundle of Meynert

divides here and crosses its fellow inside of the ganglion, and it and the ganglion degenerate after removal of the ganglia habenulæ. Not much is known of its physiological importance, but it is probably rather a stimulating than a stimulated centre of the habenular ganglia. The interpeduncular ganglion appears in all the vertebrates, being situated between the mesencephalon and the metencephalon. In the fishes it is of simple construction, and so also in the amphibians, being composed of very small triangular cells. As mentioned under "Meynert's Bundle," there are two kinds of fibres distinguishable in this fibre-connection. Of these [Honegger, <sup>23</sup> p. 408], the darkly stained ones enter into connection with the cells present in this ganglion; the more lightly stained ones go further caudad.

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# CONTRIBUTIONS TO THE COMPARATIVE MORPHOLOGY OF THE CENTRAL NERVOUS SYSTEM.

( *Continued.* )

## III.—TOPOGRAPHY AND HISTOLOGY OF THE BRAIN OF CERTAIN GANOID FISHES.—Plates XI and XIII.

It seems desirable for several reasons to introduce at this point in the series a few data relating to the Ganoid brain. The Ganoids form a natural point of departure for any minute study of the brains of the lower fishes, and if the peculiarities of structure which at first seem so irreconcilable can be shown to present no morphological difficulties, one may hope to be able to apply the homologies made out in such a typical brain as that of a lizard to any vertebrate. As a matter of fact, no better illustration of the value of morphological generalizations in the solution of special problems need be sought than that afforded by the complete and satisfactory solution of the puzzle so long unread in the case of the brain of fishes. Thus the Ganoids are found to possess a brain curiously modified, it is true, but one in which every important organ of the reptilian brain may be satisfactorily identified. The laws of development, read backward, enable us to trace the connection very satisfactorily in most cases, while the aberrant features are found to be modifications of familiar organs rather than new structures.

A brief outline is offered at this time relating to the topography and a few points only in the histology of the cephalic parts of the brain. Two types are used, and one or

both are referred to as seems most convenient. No attempt is made to give reference to the extensive literature of this subject, though a partial list of papers is appended.

The brain of the Gar-pike (*Lepidosteus*) may serve as a convenient standard of reference for fish brains. If it could have been satisfactorily studied before that of the aberrant Teleosts, science would have been saved a long period of grouping and a vast deal of confusing synonymy.

The olfactory lobes are generally unmistakable, but where, as in the cods, separated by a wide interval from the hemispheres they have been overlooked, leading to an identification of the cephalad part of the hemispheres with the olfactories. The microscopic structure of the olfactory lobes is so unmistakable that there is no excuse for the confusion. The second paired or apparently fused bodies have been very differently interpreted. Haller supposed them organs of smell, together with the hypoaria. Kuhl, Gottsche, Mayer and others homologized them unhesitatingly with the olfactory lobes. Philipeaux and Vulpian thought they represent the caruncula mammillaris of the olfactory. Tiedemann thought he discovered in them the homologues of the striata and hemispheres. Though most of the later writers have accepted some phase of this interpretation, the apparent absence of the lateral ventricles or the attempt to homologize the olfactory ventricle with them has led to great diversity in minor points. The third pair of dorsal tuberosities is often apparently single, and, though it has often been identified with the optic lobes, yet, because of a failure to recognize the thalamus (which scarcely reaches the dorsal surface in many fishes), it has been given every possible name. Very generally, among the earlier writers, it has been called the cerebrum, and the Sylvian commissure poses as corpus callosum. Two projections into the ventricles of the optic lobes have been identified as the fornix (Gottsche). Carus and Tiedemann, the one from comparative, the other from embryological considerations, identified these bodies with



the optic lobes. The histological structure, position of the optic tracts and mesencephalic nidulus of the fifth nerve, etc., make the identification certain.

The diencephalon is not usually conspicuous, though quite obvious dorsad in the gars. As though to compensate for this limitation, the ventral portion is highly developed, and from the lateral aspects of the infundibulum two pouches are formed, apparently without direct homologues in higher brains, though possibly having some relation to the mammillare. Hypophysis and epiphysis have the usual form and position, and in histological structure vary but little from the reptilian type.

The cerebellum is enormously developed, standing in relation with the relatively large size of the axial lobes of the cerebrum. The extended work of Miklucho-Maclay has done much to prevent a true understanding of the relations, especially when accepted by Gegenbaur. Overlooking the thalamus entirely, he identifies the optic lobes as the diencephalon and designates a part of the cerebellum as optic lobes, the rest as cerebellum, and the posterior part of the medulla as "nachhirn."

As will be gathered from what follows, the minute structure as well as the position of the commissures, etc., settle the homologies in most respects quite decisively.

Our present purpose requires specific reference to only the following papers, which have chiefly influenced the synonymy employed. (See end of this article for bibliography.)

WILDER, B. G. On the Brains of Fishes. *Proc. of the Academy of Natural Sciences of Philadelphia*, 1876, pp. 51-53.

WILDER, B. G. *Proc. Am. Assoc. Adv. of Sciences* for 1875.

SANDERS, A. Contributions to the Anatomy of the Central Nervous System in Vertebrate Animals. Part I, Section 1, Sub-section 1—Teleostei. *Philos. Transactions*, 1878. (This paper gives summary of literature prior to 1879.)

ALBORN, F. Untersuchungen über das Gehirn der Petromyzonten. *Zeitsch. f. wiss. Zoologie*, XXXIX, pp. 192-294, 1883.

N. GORONOWITSCH. Das Gehirn und die Cranialnerven von *Acipenser ruthenus*. *Morph. Jahrbuch.*, Bd. XIII, 1888, pp. 427-574.

HOLT, E. W. L. Observations upon the Development of the Teleostean Brain, with Especial Reference to that of *Clupea harengus*. *Zool. Jahrbuch.*, Morph. Abth., Bd. IV.

The first paper, that of Prof. Wilder, relates to the present group. We quote as follows: "The front pair of lobes [of the the fish brain] have usually, not always, been called olfactory lobes. In Myzonts or Marsipobranchs (lamprey eels, etc.), in Ganoids and some Teleosts, as in higher vertebrates they are sessile; but in many Teleosts and most, if not all, Selachians (sharks and skates) they are connected by elongate *crura* with the second lobes. These latter are almost universally called *hemispheres*. Yet the essential features of hemispheres, namely, lateral ventricles and foramina of Monro, have never been found in the second pair of lobes of any fish-like form excepting those of the Dipnoans (*Lepidosiren*, *Protopterus*, and *Ceratodus*), which seem in most respects more like those of Batrachians than of fishes. The second pair of lobes are either solid lateral laminae joined below, but with the upper borders more or less everted, as in Teleosts and Ganoids, or joined above also so as to inclose a cavity, as in Salachians. In either case the median space must be regarded as a forward continuation of the median or third ventricle, and the lateral walls as enlargements of the thalami. These enlargements Prof. Wilder proposes to call *prothalami*; in Salachians and Ganoids they are connected by more or less elongated and depressed *crura thalami* with the optic lobes behind. From the anterior part of the space between the prothalami and, in Ganoids and Teleosts, apparently in the base of the olfactory lobes, are two openings leading into the cavity of the olfactory lobes. These openings are regarded as foramina of Monro, leading into distinct, though small, lateral ventricles." "The true hemispheres of Ganoids may be represented by a raised lip of the foramen of Monro."

We think the failure to recognize the well-defined hemispheres in this case was due to the peculiar membranous

dorsal and mesal walls (pallium of Rabl Rückhard), which were not fully distinguished from the brain membranes. The proplexus, which is quite large, is sufficient to call attention to this condition. The openings lying beneath the median walls would, according to the useful system since proposed by Prof. Wilder, constitute the portæ, and the opening identified above as the porta becomes the opening of the olfactory. With these changes, and remembering that one of the most remarkable incidents of brain development has been the backward revolution of the mantle portion of the cerebrum, all the difficulties disappear, and we seek the commissures of the mantle far cephalad in front of the thin membranous portion, which seems to be homologous, in part at least, with the velum cerebri supporting the proplexus.

Rabl-Rückhard has the credit of first demonstrating the fact that the prosencephalon of fishes consists of two thick ventral ganglia, which before had been regarded as the hemispheres themselves, while the whole dorsal surface is membranous.

The most thorough investigation of the ganoid brain is the paper quoted above by Goronowitsch. Since this may not be universally accessible, a somewhat condensed translation is added of such parts as apply to the present instalment of this paper:

“*Cerebrum*.—The roof of the prosencephalon is membranous, and consists of a variously folded epithelial lamina. The roof of the olfactory lobes, however, consists of thick medullary walls. Between the roof of the prosencephalon and the epiphysis there is a broad membranous sac, the cavity of which is distally in wide connection with the cavity of the prosencephalon. The blind end of the sac is directed proximally (cephalad!). The sac, therefore, must be considered as a broad diverticle of the roof of the prosencephalon, springing from a point cephalad to the origin of the epiphysis. This may be called, for the sake of brevity, simply the dorsal sac.

“At the anterior margin of the left ganglion habenula (the left is much the smaller) a lateral induplication of the membranous roof of the prosencephalon enters the ventricle. This fold is somewhat complicated. The epithelial layer of which it consists forms numerous folds and sacs, into which projections of the membranes and blood-vessels enter. The structure is, in other words, that of a plexus choroideus.

“Careful study of continuous series of sections indicates that there is nowhere a discontinuity in the epithelial layer. The cavity of the prosencephalon is therefore completely closed. The dorsal lamina of the fold forms the ventral wall of the dorsal sac, and the ventral lamina forms the membranous wall of the prosencephalon. It thus appears that the opening of the dorsal sac is asymmetrical. Cephalad from this point the two chambers are separate. The ventral portion of the neural tube at this region consists of thick paired masses, the basal ganglia. The membranous roof bears a system of folds which becomes more complicated. The middle portion projects into the ventricle and forms a sort of falx cerebri. The dorsal wall also circumscribes the dorsal sac laterad and encloses it in a plexiform structure derived from the roof of the prosencephalon.

“Somewhat cephalad to the base of the olfactory lobes a groove appears upon the dorso-median aspect of the basal ganglia which passes mesad and can be traced directly into the cavity of the olfactory lobe. The median falx of the roof dips deeply into the ventricle of the prosencephalon. The falx extends to the epithelial lamina which connects the two olfactory lobes. Cephalad to this point the membranous roof of the prosencephalon is continued to form paired sacs dorsad to the olfactory lobes.

“In this structure of the prosencephalon of *A. ruthenus* I detect the paired nature of the prosencephalon, which consists in the strongly developed falx as well as the membranous sacs of its cephalad portion.

“At the cephalad level of the chiasm two prominences

appear upon the dorsal portion of the encephalon wall, which have the structure of the basal ganglia. This structure extends soon to embrace the entire lateral walls of the prosencephalon. These ganglia consist of a very compact, finely-granular stroma, with peculiarly arranged ganglion cells, and of a system of 'exceedingly fine, non-medullated fibres. Beneath the epithelium, in the dorsal region of the ganglia, is a layer of small cells whose fibres extend ventrad and radially. Such cells are not found in the ventral portions, but instead irregularly scattered small cells. In the midst of the ganglion are large cells with large round nuclei and pale body. The processes are here also radially disposed to the ventricular surface, producing in cross-sections a very characteristic habitus. The transition in structure in passing into the olfactory lobes is gradual.

"In transections corresponding to about the middle of the prosencephalon the basal ganglia are connected by a thick commissure—the commissura interlobularis. I preserve the older name for reasons suggested by Osborn. The mass of the commissure is composed of finely-granular substance, with scattered small nuclei. It is only in its dorsal portion that fibres may be seen crossing. It proved impossible to determine their further course. Besides these, there are a few thicker bundles of non-medullated fibres from the olfactory lobes which cross with those of the opposite side, and, passing caudad, apparently combine with the systems leading to the lobus infundibuli. The latter observation is nevertheless somewhat doubtful.

"Ventro-mesad to the optic tracts there is a well-developed system containing apparently fibres from the anterior (interlobular) commissure. The greater part is derived from the central substance of the basal ganglia. Associated with these are a number of fibres from a cluster of small nerve cells lying cephalad to the chiasm. Sagittal sections show that the lateral portions of the above-mentioned systems of fibres pass to the caudal part of the lobi inferiores. The



median and ventral portion of the system passes ventrad to the cephalic part of the lobus infundibuli. Between these are a few bundles of non-medullated fibres of the same character as those which come from the olfactory lobe and cross in the commissure. It may be suggested that the bundle in question is the direct continuation of the tract from the olfactory lobe. In the path of both these tracts there are fusiform nerve cells whose processes extend in the direction of the fibres. It is very probable that such cells interrupt some of the fibres. The above system is the chief connection between the prosencephalon and caudal parts of the brain."

The course of the *tænia thalami* is the same as usual, though it cannot be traced into the prosencephalon, probably because of its reduced dorsal walls.

Goronowitsch sums up his views upon the prosencephalon as follows:

"The cephalic ventrally arched end of the embryonic nerve tube, which, according to Götte, forms the primitive prosencephalon, is to be regarded as the most primitive phyletic condition of the prosencephalon which ontogeny suggests. The primitive prosencephalon is homodynamous with a segment of the spinal cord. By the growth of the dorsal surface of the primitive prosencephalon arose the discrete central organ of smell, while the lobus infundibuli is the result of a protrusion from its base. The formation of the olfactory centre led to the development of the prechordal portion of the skull. The architecture of the cranium of the most primitive of the Gnathostomata, the Notidaidæ, corresponds to that of the brain. The gradual development of the organ of smell gave rise to the rhinencephalon of recent Selachii. This still indifferent organ exhibits no special homologies with the diencephalon and prosencephalon of higher vertebrates. It is closely connected with the lobus infundibuli, which is reduced in higher vertebrates.

"On one hand, the reduced form of rhinencephalon of Ganoids and Teleosts is derived from the rhinencephalon of

Selachii, which, on the other hand, gives rise to the structure of the prosencephalon in Dipnoi, Amphibia, and Reptilia. It is among these forms that the first indications of the origin of the prosencephalon of higher vertebrates may be sought. The first step toward the higher organization consists in the reduction of the lobus infundibuli and a transformation of the tracts connecting with the caudal parts of the nervous system. The development of the thalami and the reduction of the lobus infundibuli alters the development process of the neural tube in higher vertebrates from the earliest stages on. There appears a diencephalic and a secondary fore-brain, the former having an entirely different significance from the posterior part of the prosencephalon of fishes, for it is the result of accelerated development of a certain dorsal portion of the neural tube which remains undeveloped in fishes. With the gradual development of the thalami and alteration of the rhinencephalon of Selachii, there gradually arise the tegmentum cruris and the pes pedunculi of higher vertebrates.

“*The Thalamus.*—The lateral walls of the lobus infundibuli form two round, lateral projections, the lobi inferiores, containing a considerable cavity. The posterior part of the lobe extends into a membranous sac, the so-called saccus vasculosus. Ventrad, the lobe connects with the bilobed hypophysis.

“The walls of the lobus infundibuli consist of finely-granular stroma, staining pink with carmine, resembling that of the peripheral portion of the cerebellum. In the peripheral portion this stroma is compact, and it requires high powers to make out a fine fibrous structure parallel to the surface. Two fibre systems are more obvious. The fibres of the first run parallel to the surface, those of the second radial to the surface. The latter spring from a layer of tissue clothing the inner surface. This layer is composed of a few series of round cells, much resembling those of the granular layer of the cerebellum. They are, however, some-

what larger than the latter, and the dark protoplasm mass surrounding the round nucleus of these cells is more highly developed. It is possible to trace the processes of these cells into the fibres of the radial system. In the fibrous zone round cells are scattered, as well as rod-like cells of the neuroglia.

“In the ventral portion of the cleft-like canal connecting the lobus infundibuli with the mesencephalic ventricle a ganglionic body composed of large cells occupies either side. Out of these ganglia springs a tract of non-medullated fibres which, passing caudad, subdivides, part of the fibres passing to the caudal part of the lobus infundibuli, and part to the dorsal portion of the sacculus vasculosus. Associated with this system is a rather large bundle of non-medullated fibres derived from a small cluster of nerve cells lying dorsad to the above-mentioned ganglion and ventrad to Meynert's bundle, immediately beneath the epithelium. The ventral portion of the caudal wall of the lobus passes into the thin epithelial wall of the saccus vasculosus, a part of the fibrous layer entering it. The saccus itself is a broad, very vascular, folded sac, clothed within by a peculiarly modified epithelium.

“The discoidal *hypophysis* consists of two completely distinct parts. The caudal portion is composed of three or four lobes, into each of which passes a thick bundle of non-medullated fibres, which pass to the ventral portion and subdivide in the several sacculi. The sacculi of the cephalic portion are covered, like the former, with multilamellate epithelium with fusiform cells, but no nerve fibres are present. The interstitial substance is connective tissue only. A thin layer of epithelium connects the two portions.

“*The ganglion habenulæ*.—Cephalad to the ganglion interpeduncular and ventrad to the transverse fibres of the commissura ansulata, there are two longitudinal bundles, which could be followed caudad only to the interpeduncular ganglia. These are Meynert's bundles, the right being much stronger

than the left. The bundles pass cephalad and mesad to the fibres of the oculo-motor, and gradually pass dorsad, and at the point of communication of the ventricle of the lobus infundibuli with the mesencephalic ventricle they lie adjacent to the epithelium. These bundles terminate cephalad to the anterior commissure in the ganglion habenulæ.

“The ganglion habenulæ is but slightly different from that of the teleosts, except for the pronounced asymmetry, which is responsible for the unequal development of Meynert’s bundles. Each ganglion consists of a central collection of granular substance, which in cross-sections appears fibrous at the periphery. The fibres converge to the median surface of the ganglion and form a commissure uniting the ganglia. The central substance is surrounded by several layers of granular cells, which greatly resemble those of the lobus infundibuli. The plasmatic body surrounding the large round nucleus is more highly developed, and its produced poles are radial to the surface. These cells send their processes into the central substance, even to the middle of the ganglion. The dorsal surface of the ganglion has a thinner layer of granular tissue than the ventral, which is separated from the central substance by a layer of longitudinal fibres. The chief portion of these fibres belongs to Meynert’s bundle; the smaller portion collects from the ventral portions of the brain walls. The radial fibre systems which spring from the granular cells of the ventral layer are divided into small bundles by the fibres just described. In the feebly developed left ganglion the ventral granular cells lie directly upon the central substance. The fibres of Meynert’s bundle, as well as the fibres of the ventral part of the brain walls, are dispersed in the central tissue of the left ganglion.”

*Lateral ventricles.*—The lateral ventricles are not absent, as Wilder supposed, nor are they merged in the olfactory ventricles, as stated by others.<sup>(1)</sup> Fig. 1, Plate XI, taken at a

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1 SANDERS, op. cit., p. 768: “The cerebral lobes homologize the corpora striata,

point in front of the foramen of Monro in the sturgeon brain, shows that a cavity clothed by tela choridea (or pallium) extends cephalad along the dorso-mesal surface of each olfactory lobe. This cavity is of great morphological importance; part of its walls are modified to form a plexus, and it comes into direct communication with the aula. The surface of the lobe bordering is, like other ventricular surfaces, covered with epithelium. The cellular structure is also unlike that of the remainder of the lobe. It seems unquestionable that this space is homologous with the cavity of the lateral ventricle, which is not roofed over with nervous matter, but has merely the tela or pallium. These two ventricles become confluent cephalad to the openings of the olfactory lobes, but a partial division, by a depending loop corresponding to the dorso-mesal walls of the mantle, may be traced back of that point. From the ventral extension of these median walls two arms, forming with them an irregular inverted Y, pass laterad nearly to the ectal thickened walls of the hemisphere, shutting off a median aula from the lateral ventricles, with which the former is connected by large portæ. It is from the ventricles thus bounded, and not from the median chamber, that the olfactory aqueduct springs.

The development of nervous matter in the cerebrum is greater relatively in the gars, therefore the membranous portion of the mantle is greater in *Scaphirhynchus*. In *Lepidosteus* the ventricle gives off two spurs in the median portion delimiting a body somewhat resembling the corpus lenticulare of the striatum. The posterior cornu sweeps back of the crura and then circumscribes the ventral and ectal portions of the cerebrum, finally meeting the dorsal extension of the ventricle, enclosing a large occipito-basal lobe much as in reptilia. The extent of the ventricle may be most

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combined with the hemispheres of the brain; and although I have not discovered in the species examined by me the ventricles in those bodies described by Wilder, yet I do not doubt that in other species they may exist."



easily recognized by the epithelial covering of the axial lobe where it is present.

The conversion of the free portion of the mantle to a functionless membrane is carried to its extreme in fishes, but birds furnish many resemblances.

The cerebrum is more highly developed in *Lepidosteus*. Cephalad, it projects beyond the olfactory, and appears in transection as two independent bodies dorsad to the olfactory lobes. Plate XIII, Fig. 1, illustrates a section through the olfactory and extreme cephalic part of the lateral ventricle, which is bounded only by the pallium. The relations are essentially the same in all ganoids. Fig. 2, which passes through the corpus callosum, shows the relation between the olfactory aqueducts and lateral ventricle. The real homologues of the foramina of Monro are considerable slits. In the sturgeon, as may be gathered from Plate XI, Fig. 2, the relations are similar, but the partial eversion of the hemispheres laterally brings the opening of the aqueduct of the olfactory lobes farther laterad.

In the figure, because of some distortion in the section, the median walls of the ventricles have been rendered asymmetrical, and the openings of the foramina of Monro appear too large.

In Fig. 3, of the same plate, the median walls are occupied by the plexus, which is shaded dark.

The middle portion of the hemispheres are somewhat quadrangular in transection (Plate XIII, Fig. 3). Cephalad, the dorsal portion projects laterally considerably, while further caudad the lateral aspects are nearly perpendicular. The two hemispheres become separate at the chiasm, the connection being formed by a portion of the velum, united with the cephalo-lateral aspects of the habenæ.

Respecting the *dorsal sac*, *Lepidosteus* affords much clearer information than the sturgeon, and renders necessary a considerable change in the interpretation of this structure, offered by Goronowitsch. Morphologically it is a dorsal

pouch of the diatella, such as may be detected in all reptiles in which the epiphysis is strongly developed. The asymmetry upon which Goronowitsch lays so much stress is slight, and more apparent than real. The fact that it extends so far cephalad between the hemispheres, is an incident to the cephalad projection of the epiphysis. It may be useful to first study the structure of the latter.

The *epiphysis* springs from the most caudal portion of the recessus pinealis, which is clothed, as usual, with very large and dense epithelium, very different from that of the adjacent parts of the third ventricle. There seems to be a perforation passing obliquely dorso-caudad, forming the communication between the cavity of the epiphysis and the recessus. The epiphysis itself is tubular, and arches rapidly caudad to a point over the tectum, then curving more rapidly cephalad, between the hemispheres, is slung, as it were, in the membrane connecting them. The structure is like that of reptiles, varying much in different localities by the greater or less development of certain elements. In characteristic portions, there is, first, the wall of connective tissue; seated upon this are slender cells, fibrous in character, which support small granular nuclei in several series, and centrally a larger nucleus beyond which the cell extends as a long narrow flagellum projecting into the cavity. The appearance is as though the single stalk supports nuclei of both sorts, though this may be an illusion. Nerve fibres may be followed in the spaces between the cell bases, extending in the direction of the axis of the organ, and passing into the larger nuclei. There can be no doubt of the nervous character of the organ.

A blood sinus closely invests the epiphysis, outside of which is a second investment from the dorsal sac which projects caudad to ensheath it. The walls of the dorsal sac consist of a single-layered epithelium with long cilia or flagella projecting into the lumen. Numerous plexiform diverticles also project into the cavity. The fibres from the

epiphysis were traced, with apparent certainty to the supra-commissura.

Cephalad to the habenulæ, as well as immediately above them, the dorsal sac communicates with the third ventricle, the lateral ventricles being entirely distinct. Slightly further cephalad the dorsal sac, is shut off from a median portion which must be considered as homologous with the aula. Into this median portion the cavities of the lateral ventricles open, as usual, the only difference being that the aula is more elongated than usual, and the portæ are correspondingly enlarged. It has sufficiently appeared from the above that the dorsal sac is not a portion of the cavity of the prosencephalon, but of the diencephalon. It is not a new structure, but one found in reptilia as well, and pertains to the epiphysis.

In *Scaphirhynchus* the relations are essentially the same, though the plexiform development along the median wall is much greater, and the epiphysis is scarcely as large. The caudal portion of the dorsal sac is smaller, and an irregularity is introduced by the greater size of the right habena.

The less retro-development of the hemisphere may explain why the epiphysis is not arched so far caudad as in *Lepidosteus*.

Serious exception must be taken to the use of the term "falx" for the median projection of the pallium or dorsal roof of the cerebrum. There can be no reason for rejecting the homology between the membranous roof of the cerebrum in fishes and the mantle part of the cerebrum. The extent to which cellular elements develop in the walls of the embryonic nerve tube varies within the broadest limits. The birds have a great reduction in the cellular mantle structures. The median portion of the pallium must be homologous with the median or interventricular portion of the mantle in other vertebrates. The portion of the investing membranes, which is associated with this fold, must represent the falx.

*Histology of the Brain of Lepidosteus and Scaphirhyn-*

*chus*.—In *Scaphirhynchus* the *olfactory lobes* are ovoid tuberosities upon the cephalo-lateral aspects of the hemispheres, with their longer diameter in the axes of the strongly divaricated olfactory nerves (Plate XI, Fig. 15). Cephalad, they are completely closed, and a considerable ventricle occupies the centre (Fig. 1, Plate XI). Caudad, where they pass into the cerebrum, they stand in communication with the hemispheres, and are roofed over only by the thin pallium or dorsal lamina of the cerebrum.

The histological structure is similar to that in reptiles, save that the specific cells are relatively more elongate and more sparingly distributed, nowhere forming a connected layer. The glomerular layer is highly developed, and there is a noticeable absence of the Deiter corpuscles, so usual an accompaniment of the glomerules. The neuroglia layer, between the glomerules and the inner granular zone, is wide, and contains few very irregular elongated cells with large, pale, round nuclei.

These cells are of the most various forms, often having a long, apical process, and two or more basal processes, but the relations may be reversed. Frequently these cells are seen between the massed glomerules, occupying the irregular interspaces. There are also cells of irregular shapes and more deeply stained, which are scattered among the above. These are, perhaps, to be compared with the rhinomorphic cells elsewhere referred to. The granular zone is well developed. The epithelium is many-layered.

In sections of *Scaphirhynchus* caudad to the point where the olfactory opens into the lateral ventricle (Plate XI, Fig. 3), there is a rapid eversion of the hemisphere, causing the olfactory portion to be carried ventrad and laterad. A small groove separates a projection which is adjacent to the olfactory from the basal portion of the hemisphere (see right side of the figure quoted). This may be called the ala, and it contains concentrically arranged cells. The segment of the cerebrum remains distinct in structure from the basal portion.

The olfactory structure comes soon to lie entirely ventrad to the ala and then disappears.

In *Lepidosteus* the relations of the olfactory to the cerebrum are quite different (compare Plate XIII). Here the olfactory lobes extend in the same vertical plane as the cerebrum, but are obliquely applied to the ventral aspect of the hemispheres, extending well toward the chiasm. The glomerular structure extends far back, especially mesad, but is overarched laterad by a densely cellular descending portion from the dorsal region of the cerebrum. From this ectal layer fibres appear to converge to the callosum (Fig. 2, Plate XIII).

At about the level of the callosum the lateral aspects of the olfactory lobes, beneath the cortical invasion above mentioned, there accumulates a large cluster of olfactory cells which may be traced caudad some distance beyond the olfactory ventricle.

It will be convenient to begin the study of the cerebrum by reference to the structure of a section cephalad to the chiasm and caudad to the olfactory.

The transection at this point is somewhat quadrangular, being broadest dorsad. The hemispheres may each be divided, for convenience, into a basal and a lateral portion. The two hemispheres are connected by a small intermediate portion which must be regarded as morphologically equivalent to the lamina terminalis, and consequently the cephalic portion of the thalamus.

The portion of the ventricle adjacent to this thalamus segment differs in the appearance of its epithelial lining from the lateral ventricle. The median walls of the pallium descend to near this level

The cellular structure of this segment is also unlike that of the cerebrum, consisting of small, clear nuclei with granular contents and pale body, which can rarely be made out in these preparations.

The basal portion of each hemisphere contains a circular nidulus consisting of the cells which form the caudad con-



tinuation of the cell cluster which envelops the olfactory. The centre of the nidulus is filled with non-medullated fibres and a few small cells. The cortical portion is composed of densely clustered fusiform cells with round, clear nuclei. These cells are less than half the size of those which occupy the centre of the lateral portions. The lateral and ventral part of the basal portion is occupied by a broad band of neuroglia, with numerous non-medullated fibres passing apparently toward the anterior commissure.

The lateral portion of the hemispheres consists of a more or less quadrangular segment, bordered dorsad and mesad by the ventricle; laterad it forms the wall of the brain, and ventrad it is in direct contact with the basal portion just described. From this portion it is separated laterad by a fibre tract which, in transverse section arches ventrad from the lateral surface to the nidulus of the basal portion. Ventrad to it and apparently associated with it is the system of concentric fibres, already described upon the periphery of the basal portion. Dorsad, this tract may be traced along the entire lateral periphery of the lateral lobe. Immediately dorsad and mesad from the tract there are a number of small, dark pyramidal cells, with their long axes toward the periphery. Similar cells are crowded at the dorso-lateral angles. The entire dorsal and mesal portion of this part of the cerebrum is filled with from six to ten irregularly concentric series of fusiform cells. These are of moderate size, and are characterized by the circular, clear and granular nuclei, and by the pale protoplasm of the body, which varies greatly. Often the form is flask-shaped, with one strong process peripherad, and several from the blunt end extending toward the ventricle. Along the median portion of the ventricle the number of rows is reduced, and the character of the cells changes. Here the cells are much larger and more multipolar in form, still preserving the same general character otherwise.

It is obvious that it is this region which proliferates the large æsthesodic cells of the central portion of this region

of the cerebrum. These latter are the largest and most characteristic cells of the cerebrum, being fusiform or multipolar in outline. Without attempting any special homologies of the regions indicated with the lobes already described in the cerebrum of reptiles, it becomes at once obvious that there is a great similarity in the disposition of cellular elements. The cephalo-lateral aspects contain pyramidal cells, the ventro-median fusiform, while the interior of the axial lobe contains a paraxial æsthesodic variety. It would appear, then, that regions corresponding to the parietal lobes of Sauropsida exist in fish brains. That these regions of pyramidal cells are motor, is farther indicated by the strong tract arising in this neighborhood.

Caudad to the section just described the thalamus expands; and a pouch of the third ventricle is formed above the chiasm with its opening caudad. At the chiasm the ventral walls of this supra-chiasmic fossa are driven laterad and become filled, next the ventricle, with densely-packed cells. In passing caudad the basal portion of the cerebrum gradually becomes more distinct, until it attains a measure of independence and is finally overarched by a diverticle from the lateral ventricle.

By reason of its connection with the olfactory, and its position, this lobe may be compared in a general way with the hippocampus.

The caudal portion of the lateral lobe is circumscribed by a diverticle of the ventricle, and becomes completely homologous with the occipito-basal lobe of reptiles.

*Commissures of the Cerebrum.*—The exact equivalence of the commissures of the cerebrum is a matter of much difficulty in these fishes where the whole dorsal and median portion of the tectum cerebri or mantle portion is apparently represented by the pallium cerebri. Considering, however, that the direction in which the cerebrum has been differentiated in higher animals is caudad, and that, in the lower brains, bodies which lie caudad or dorsad in higher vertebrates must be sought dorsad or cephalad, it is not difficult to

homologize the pallium with the plexus-bearing projection from the posterior and mesal margin of the mantle. Since the plexus in this case occupies the vertex, instead of projecting from the caudal region, all structures morphologically cephalad to the plexus must be sought still further cephalad or ventrad. Using this clue, and observing that the cerebral cortex folds ventrad over the olfactory structure, we think we find a homologue of the calloso-hippocampal commissure connecting the two halves of the cerebrum cephalad to the openings of the olfactory crura into the common ventricle, and lying just entad to the membranous lamina terminalis (Fig. 2, Plate XIII). The bundle is very small and seems to contain a few fibres from the olfactory regions, as well as others from the cephalic portions of the cerebrum. No indication of the callosum was seen in *Scaphirhynchus*.<sup>(1)</sup>

Regarding the *anterior commissure* there can scarcely be a mistake, as it is a very strong though disperse band of fibres lying in the ventral fused portion of the cerebrum cephalad to the chiasm and cephalo-dorsad to the supra-chiasmic fossa of the third ventricle, and thus well in front of the crura cerebri. This commissure has been generally recognized by later writers, while the callosum seems to have been overlooked. See above for description of the anterior commissure (*C. interlobularis*) by Goronowitsch.

*Tracts from the Prosencephalon.*—We are unable to agree with Goronowitsch in his remarks upon the thalamus and the tracts connecting it with the cerebrum. So far from the pedunculi being absent in ganoids, the gars at least have the tracts as highly developed as could be expected where the gray matter is in so relatively small amount.

The motor tracts which accumulate along the lateral aspects of the prosencephalon collect, as already described, to form curved tracts dorsad to the basal lobe (homologous

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<sup>1</sup> HOLT, l. c., mentions what he calls an olfactory commissure in the herring, which may prove to be the same structure as that above described. He does not appear to have thought it possible to homologize it with the callosum.

with the postrhinal lobe of mammals), thence crossing in the anterior commissure precisely as in the opossum. The tracts then lie on either side the ventricle. The supra-chiasmic fossa of the third ventricle fuses with the main portion of the ventricle a short distance caudad to the præcommissura. At that point and for some distance caudad these motor bundles lie in the central regions of the thalamus near the ventricles.

A large number of sensory fibres accumulate in the lateral aspects of the basal lobes and with the olfactory fibres pass into intimate relations with a dense granular nidulus. Apparently receiving numerous fibres from the hippocampus portion of the occipito-basal lobe, which also has a strong tract connecting with the cephalic part of the hemisphere, this compound sensory tract passes, *without crossing*, into the lateral regions of the thalamus and, passing in the opposite direction from, but nearly parallel to the optic tract, reaches a ventral portion of the thalamus in the cephalic part of the infundibular region. A part of the sensory fibres turn laterad beneath the corpus geniculatum and enter the hypoarium. The motor tracts continue in the central portion of the thalamus.

A special tract comparable with the fornix was not observed, though some of the fibres passing to the hypoaria might be compared with it. The tract of dark fibres passing from the median part of the infundibular lobe and the dorso-median portion of the hyporaria to niduli beneath Meynert's bundle might be likened to the bundle of Vicq d'Azyr.

*The Gray Matter of the Thalamus.*—The thalamus extends somewhat cephalad to the anterior commissure and beneath the latter in the walls of the supra-chiasmic fossa. The cells here are in several series near the ventricle and are of the usual fusiform sort. The peduncles with both sensory and motor tracts pass into the thalamus at its latero-dorsal aspects. Immediately caudad to the point where the peduncular connection ceases, a small nidulus of rather large, pale

cells makes its appearance, apparently connected with the sensory bundle. It is bounded laterad by the optic tracts and dorsad by the *tænia thalami*.

Immediately caudad to the chiasm the large *corpus geniculatum* appears upon the ventro-lateral aspects of the thalamus and occupies a position ventrad to the optic tracts for their whole length. The cells are irregularly scattered and of the fusiform variety.

Somewhat further caudad there appears a peculiar cluster of deeply staining cells ventrad to the geniculatum. The cells of this nidulus are extremely irregular and quite large, with long branching processes, and they are arranged in no definite direction, yet the apical processes are chiefly turned from the periphery. A part of the cells lying massed near the surface have a rather fusiform character and seem to constitute a distinct portion. This nidulus may be designated as the nidulus *præcinereus*, although its homology with the anterior nidulus of the cinereum of mammals remains to be proven. A very similar cluster of cells occurs in reptiles near the *crura*, as also in the opossum.

The *habenæ* is imperfectly divided into two parts, a ventro-median portion, with smaller cells, giving rise to Meynert's bundle, and a cephalo-dorsal and ectal portion, of larger cells, giving rise to the *tænia*. The right *habenæ* is somewhat larger and is apparently chiefly associated with the fibres of the epiphysis.

The *hypoaria*, or lateral lobes of the cinereum, are less highly developed in *Lepidosteus* than in the sturgeon. They arise caudad to the chiasm as tuberosities of the lateral wall of the infundibulum dorsad to the ventral nidulus of large cells above mentioned. A diverticle of the infundibulum enters them, and this cavity expands to a spheroidal cavity. The cell structure is similar to that of the tuber. In *Lepidosteus* they extend much farther caudad, so as to reach the exit of the third nerve. A rather strong tract enters the caudo-mesad portion where it is becoming separated from the



thalamus and passes toward the tract of the third nerve, passing Meynert's bundle, and apparently unites with fibres passing toward the cerebrum. If these fibres be compared with the fornix tract, they might seem to warrant the suggested homology of the hypoaria with the mammillaria. This seems the more reasonable inasmuch as there seems to be a homologue of the corpus geniculatum dorsad to them.

The *third ventricle* varies somewhat from the form found in Acipenser. In the region of the infundibulum it is a long slit, opening above into the dorsal sac and connecting by a narrow triangular opening dorsad with the cephalic section of the ventricle. Ventrad, there is a short cephalad diverticle, so that transections in front of the habenæ present the appearance of having the two halves connected by a soft commissure. After passing for a short distance cephalad, the ventricle again passes to the ventral surface and extends forward into the supra-chiasmic fossa. It would appear that all that would be necessary to produce a real soft commissure would be the opening of a communication between the ventral portion of the two segments of the third ventricle. Caudad, the ventricle gives rise to the ventro-median ventricle of the saccus vasculosus and two lateral ventricles of the hypoaria.

The *third and fourth nerves* have the usual relations, though somewhat complicated by the inward growth of the cerebellum. In the sturgeon (Plate XI, Fig. 7) the third nerve can be traced, from its nidulus near the floor of the aqueduct not far from the median line, ventrad to its exit, from which point it passes laterad. In *Lepidosteus* it pursues a more curved course and emerges in the space between the hypoaria and dorsad to the overlapping part of the cinereum, thence arching caudo-laterad about the neck of the hypoaria, and turning cephalad, it occupies a small groove in the lateral aspect of the thalamus dorsad to the hypoarium.

The fourth nerve crosses in the valve and escapes in the

groove behind the optic lobes, following the usual course thereafter.

The *optic tracts* may be traced caudo-dorsad along the thalamus to the mesencephalon, where they divide into a median and a lateral portion. These are doubtless continuous superficially, but are separated in the plane of the section by the corpus opticum, as in birds.

The *posterior commissure* occupies the usual position. It is over-arched by the cephalad projection of the optic lobes (see Plate XIII, Fig. 5) in which the *Sylvian commissure* occupies the usual position. The relations are somewhat obscured in *Scaphirhynchus*.

The *lobi optici* are very large and resemble those of reptiles in nearly every respect. Very large ventricles occupy their centres, and where these are confluent (Fig. 9) there is a curious pendant body on either side of the median line due to a lateral diversion of the median walls of the tecta, below their union with each other. This body, originally called fornix by Carus, may perhaps retain the name suggested by Fritsch, *torus longitudinalis*, since it is free from the false homology involved in the other. The structure of this body is very simple, consisting of dense clusters of small cells like Deiter's corpuscles.

The surface of the tectum (1) is clothed with a very thick neuroglia layer, beneath which (2) is a rather narrow uniform band of the superficial optic fibres. Within this (3) is a broad band, containing peripherally a few radially arranged elongate pyramidal cells. Quite near the ventricle (4) is a multiple or single series of small pale fusiform cells, with circular nuclei and interspersed Deiter's cells. The ventricle is lined with the usual epithelium, (5) the fibres from which radiate to the surface of the tectum, bearing, as in reptiles, distinct inoblastic nuclei. The above are the primary divisions of the tectum, but are susceptible of farther subdivision on the basis of the course pursued by the nerve fibres in each. Just ectad to the zone of small cells

(4) is a tract of nerve fibres passing to the "crura of the optic lobes" or ental optic tract. The outer part of (3) might be divided in the same way. For a description of the minute structure of the tectum in teleosts, see Sanders.<sup>(1)</sup> Bloodvessels are very numerous, indicating a high degree of activity in this region. The necessary regenerative or nutritive cells seem to be collected in the tori.

From the base of each optic ventricle there is a projection which has been called *torus semicircularis*. Sanders says:<sup>(2)</sup> "The tori semicirculares may be considered as the anterior termination of the medulla oblongata; they are tuberosities of a more or less semicircular shape, which project into the floor of the ventricle of the optic lobe; they are principally composed of grey matter, through which the bundles of the crura lobi optici pass on their way to the internal surface of the tectum." To this it is to be said that these lobes must be regarded as an inherent part of the mesencephalon, being provided with a slightly modified ventral accumulation of the cell-layer constituting the fourth of the above-mentioned layers of the tectum. The structures are those already familiar in reptiles, and called (rather unfortunately) by Rabl Rückhard the *colliculi*.<sup>(3)</sup>

The roof of the aqueduct is thickened and thrust far forward under the optic lobes, or better, the optic lobes are thrust so far caudad that they over-arch the valve of Vieussens or *valvula cerebelli*. The presence in this body of the decussation of the fourth nerve is sufficient proof of the correctness of the homology.

In the sturgeon the relations are greatly disguised by the forward protrusion of the great medio-cephalic lobe of the cerebellum within the common ventricle of the optic lobes.

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1 L. c., p. 751.

2 L. c., p. 754.

3 SANDERS, op. cit., p. 768, "the torus semicircularis I would, with some doubt, refer to the corpus geniculatum externum." Fritsch regarded the deeper part of this body as the corpus quadrigeminum and the superficial part as the thalamus.

The valve thus becomes restricted and the cephalic lobe of the cerebellum is rolled upon itself (Plate XI, Figs. 7, 8). One result of this modification is the great distension of the optic ventricle and commensurate thinning of the tectum posteriorly. The colliculi are also reduced in size thereby.

In *Lepidosteus* the adhesion of the valve dorsally upon a forward tongue of cerebellum ventrad is considerable, but in *Accipenser* the ventral (cerebellar) portion is pushed forward and rolls cephalo-dorsad, fairly filling the cavity. The structure of this body, which may be called *volvula cerebelli* or *volvula*, is identical with that of the cerebellum proper.

*The Cerebellum.*—In the development of the cerebellum we have the most characteristic feature in the brain of the ganoid fishes and, at the same time, the peculiar modifications of the theme express the generic variations most distinctly. In the gars, where the whole brain is quite reptilian, the cerebellum is highly developed superficially, while in the sturgeon only a relatively small part is exposed, the remainder being packed in the cavity of the mesencephalon and the laterally enlarged fourth ventricle. In *Lepidosteus* the cerebellum may be divided into the following parts: first, a cephalad invasion of the mesencephalic cavity, more or less closely associated with the valve, constituting the *volvula* as above described; second, the median lobe or *vermiform lobe*, third, two *lateral lobes*; fourth, a posterior pouch or *bursa*.

As a whole, and excepting the *volvula*, the cerebellum resembles that of the alligator. The vermiform process is moderately convoluted, so that in longitudinal section there is anteriorly a caudad invagination, then a cephalad projection carrying a part of the ventricle forward as an anterior recess lying dorsad to the pocket formed from without, due to the invagination or concrescence above-mentioned. The main cavity of the vermiform lobe is pentagonal in transection, giving off diverticles into the cavities of the lateral lobes.

The lateral lobes in a median transection of the cerebellum form two large projections laterad, somewhat more than half as large as the vermiform process dorsad, and about half as large as the medulla ventrad to it. At this point the recessus lateralis of either side (not to be confounded with the ventricle of the lateral lobes) makes its appearance, being closed with the usual velum or protrusion of the endyma. This membranous sac is small as compared to the development in the sturgeon (Plate XI, Fig. 10).

In *Scaphirhynchus* the volvula is enormously developed and thrust far forward, completely obscuring the valve. Appearing first as a pentagonal projection from the inner (dorsal) surface of the (inverted) valve, it goes on increasing cephalad, till, rolling ventrad, it folds upon itself, turns caudad, carrying its median protuberance upon its (now ventral) surface, and passing somewhat dorsad to connect with the vermiform lobe. The central portion consists of white matter filled with enormous and beautiful branching Purkinje's cells, the lateral portions containing the Deiter's corpuscles. There is no bursa nor distinct cephalad diverticle, as in *Lepidosteus*, but the vermiform lobe remains a solid mass with its white matter mesad and dorsad and its granular layer laterad and ventrad to the end (Fig. 11, Plate XI).

The lateral lobes are enormous and contain small ventricles. Caudad, the dorsal portion is separated by the formation of the large recessus lateralis (Fig. 10, Plate XI) and becomes a wing-like expansion of the vermiforme. The ventral portion adheres to the latero-dorsal margin of the fourth ventricle, retaining its characteristic structure far caudad. Cephalad, the lateral lobes are perforated by several nerve roots as beyond (Fig. 9, Plate XI).

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#### NOTE TO PLATES X AND XII.

In the previous instalment of the article entitled "Contributions to the Comparative Morphology of the Central Nervous System," reference was made in several instances to plates which it was impossible to distribute with that number. In making up the present number it became necessary to rearrange the figures upon the plates, causing the following changes:

For "Plate X, Fig. 5," read "Plate XII, Fig. 10."

For "Plate X, Fig. 14," read "Plate X, Fig. 9."

Elsewhere substitute "Plate XII" for "Plate X."

For "Plate XII, Fig. 3," read "Plate XII, Fig. 8."

On page 27, for "Fig. 7, Plate III," read "Plate X, Fig. 6."

#### PLATE X.

##### HISTOLOGY OF THE BRAIN OF THE LIZARD, SNAKE, AND TURTLE.

*Fig. 1.* Purkinje's cells from the cerebellum of the lizard.

*Fig. 2.* Cells from near the caudal margin of the pyriform lobe of the black-snake.

*Fig. 3.* Portion of the intra-ventricular lobe of the lizard, drawn with the aid of a one-fifteenth inch objective and camera.

*Fig. 4.* Cells from the caudo-lateral part of the tuber cinereum of the black-snake, with one-fifteenth inch objective.

*Fig. 5.* Cells from Gasser's ganglion.

*Fig. 6.* Transection of epiphysis of the lizard.

*Fig. 7.* Portion of the caudal part of the cerebral mantle near the ventricle, to illustrate the nature of the neuroglia.

*Fig. 8.* Motor and sensory cells from frontal cortex of lizard.

*Fig. 9.* Structure of the pyriform lobe of lizard brain, with rhinomorphic and proliferating sensory cells.

*Fig. 10.* Portion of a longitudinal section of the optic lobes of the turtle, showing cells of fifth nidulus.

## PLATE XI.

*Figs. 1-12.* Transections of the brain of *Scaphirhynchus*.

*Fig. 1.* Section of the olfactory lobe. Dorsally the cephalad extension of the lateral ventricle occupies the median aspect. Laterally the olfactory nerve fibres are emerging.

*Fig. 2.* Portion of transection of the anterior part of the cerebrum. The median walls of the ventricle are not naturally represented, partly because of obliquity and distortion of the section. The opening of the olfactory ventricle is into the lateral ventricle, which is connected with a median aulla by the foramina of Monro.

*Fig. 3.* Section near the posterior margin of the olfactories, somewhat oblique, so that the right side passes through the olfactory while the left cuts the aulla alone. The aulla on the right side lies dorsad to the olfactory, and is separated from the basal portion of the cerebrum by a fissure.

*Fig. 4.* Section through the superior commissure; the loop of the membrane to the left is to be ignored. The hypoaria occupy the whole ventro-lateral aspects.

*Fig. 5.* Section through the posterior commissure. *M. b.*, Meynert's bundle.

*Fig. 6.* Section through the optic lobes. The ventricles of the hypoaria are confluent.

*Fig. 7.* Section at the exit of the third nerves. The volvula occupies the cavity of the optic lobes.

*Fig. 8.* Section near the anterior margin of the medulla.

*Figs. 9-12.* Sections farther caudad.

*Fig. 13.* Cells from the apparent origin of the third nerve.

*Fig. 14.* Cells from the cerebellum.

*Fig. 15.* Ventral surface of the entire brain.

## PLATE XII.

*Figs. 1-3.* Portion of horizontal sections of the black-snake brain, to show the relations of the præcommissura, callosum, fornix, etc. *Fig. 1* lies farthest ventrad. *f.*, fornix; *b.o.tr.*, occipital portion of the præcommissura; *l.f.*, parietal portion; *ac'*, frontal, or "olfactory" portion. Compare with *Figs. 7* and *8*.

*Fig. 4.* Cells from the Gasser's ganglion of the turtle.

*Fig. 5.* Longitudinal perpendicular section through the middle of the hemispheres of the brain of an embryo of the black-snake.

*Fig. 6.* Longitudinal horizontal section of the brain of a black-snake.

*Fig. 7.* Diagram to illustrate the principal tracts and niduli of the brain of the black-snake, formed by the composition of several sections. *o.c.*, olfactory cortex; *i.e.*, that portion of the cortex lying upon the crus olfactorii; *o*, tract connecting the above with the frontal region; *c.c.*,



corpus callosum; *ac'*, *ac''*, *ac'''*, frontal, parietal and occipital portions of præcommissura; *f.*, fornix; *t.t.*, tract from the tænia thalami into the thalamus.

*Fig. 8.* Section somewhat cephalad to Fig. 9. *H.*, habena; *M.*, nidulus Meynerti; *N.*, substantia nigra; *B.*, nidulus of the substantia nigra; *P.*, peduncles.

*Fig. 9.* Transection through optic lobes and infundibulum of the lizard. *c.S.*, commissura Sylvii; *P.c.*, postcommissura; *p.*, pedunculi; *op.tr.*, optic tracts.

*Fig. 10.* Median longitudinal section of an embryonic black-snake brain, (see Fig. 5), to show the relation of the epiphysis to the habena, membranes, and skull.

*Fig. 11.* Section through the cerebellum of one of the same set of embryos near the caudal extremity, to illustrate the proliferation of Purkinje's cells. (Compare Fig. 14.)

*Fig. 12.* Section through the same brain at the base of the cerebellum at the exit of the trigeminal nerve.

*Fig. 13.* Similar section at the exit of the eighth, which, by reason of its slight obliquity, also displays the course of the seventh nerve.

*Fig. 14.* A portion of a section adjacent to that of Fig. 11, at the angle of the ventricle, illustrating, as is supposed, the proliferation of Purkinje's cells from cells associated with the ventricular epithelium.

*Fig. 15.* Pyramidal cells from the motor region of the brain of a lizard.

#### PLATE XIII.

*Figs. 1-8.* Transections through the brain of the Gar-pike, *Lepidosteus*.

*Fig. 1.* Olfactory lobe. *v.l.*, cephalad projection of the lateral ventricle, roofed over by the velum.

*Fig. 2.* Transection at the callosum, *c.c.* *v.l.*, lateral ventricle; *m.*, membranous roof of the ventricle corresponding to the mantle; *a.l.*, axial lobe of the cerebrum; *f.M.*, foramen of Monro; *gl.*, remnant of the glomerular layer of the olfactory; *n 1*, olfactory nidulus beneath the aqueduct of the olfactory.

*Fig. 3.* Transection back of the chiasm. A mesad protuberance of the axial lobe corresponding to a part of the striatum is separated by projections of the ventricle. The aulla is partly confluent with the ventricles. *v.l.*, spur of the posterior cornu passing cephalad. In the connecting portion uniting the thalamus and hemispheres some evidence of the tænia thalami was detected.

*Fig. 4.* Transection at the level of the habenæ. The lateral ventricles have completely circumscribed the axial lobe. *c.g.e.*, corpus geniculatum externum; *n*, lateral nidulus of the thalamus; *Hy.*, hypophysis; *n.M.*, nidulus Meynerti; *f.M.*, foramen of Monro.

*Fig. 5.* Transection through the posterior commissure. A portion

of the epiphysis is seen above, *cp.* *S.c.*, commissura Sylvii; *Pc.*, post-commissura; *M.b.*, Meynert's bundle; *Ha.*, Hypoarium.

*Fig. 6.* Transection at the middle of the optic lobes. *III*, third nerve in a groove between the hypoaria and lateral lobe of the thalamus. The tori project medianly into the ventricle.

*Fig. 7.* Transection through the posterior part of the optic lobes. *IV*, fourth nerve; *vol.*, volvulus, or portion of the cerebellum thrust into the optic ventricle.

*Fig. 8.* Transection through the medulla and cerebellum at the opening of the recessus lateralis.

*Figs. 9-10.* Dorsal and ventral views of the entire brain of the gar. The bi-lobed mass lying behind the cerebellum is not of a nervous character.

## EDITORIAL.

### NEUROLOGY AND PSYCHOLOGY.

It is but natural that a marked transformation in externals should awaken expectation of corresponding improvement within. A pretentious gateway immediately creates visions of a roomy château. But in our day, improvement is frequently long delayed at the surface, and the elegant garments and equipage of Mrs. Newrich afford an erroneous indication of her mental equipment. Nor do we gain much consolation from the knowledge that her daughters have acquired at least the affectations of culture.

The case is somewhat so with regard to psychology. The study of brain and nerve is recognized as the gateway of psychology, and the enormous though heterogeneous body of the science of neurology, which has grown up in the last twenty years, may legitimately lead us to expect a commensurate advance in the inner domain. But psychology, after long hesitating to avail itself of the help thus offered, has apparently been able to do little more than clothe itself in the garb and acquire the language of neurophysiology. It may be useful to cast a glance backward and observe some of the steps toward the recognition of physiology by psychology and the consequent reinterpretation of metaphysics.<sup>(1)</sup>

The first modern attempt at such a reconciliation is linked with the name of René Descartes, who, at a time when the

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<sup>1</sup> For part of the material here employed I am indebted to the paper of Professor Wilhelm Wundt, entitled "Gehirn und Seele," forming a part of his well-known volume of popular essays.

awakened intellect surged everywhere over the weakened ecclesiastical barriers, was content to view the struggle across the moat of his château at Fraueker and to contribute to the conflict indirectly so far as personal safety permitted.

In a time when the Copernican astronomy deprived man of his commanding position at the heart of the universe, but opened a vaster though humbler arena to his intellect, when Gallileo was formulating the laws of motion, and when Harvey had awakened the hope of affording for the activities of the body a similar mechanical explanation, it was quite natural that the attempt should be made to discover a mechanical explanation for the phenomena of mind.

Influenced by Baconian teaching, Descartes insists upon a basis for speculation in observation, though his philosophical system seems to show so little evidence of it and stands forth in systematic completeness and logical unassailability strikingly contrasted with his famous fundamental doubt.

It is evident that in his study of the relation of soul and body, which he regarded as one of his most important achievements, and whose effects have long outlived his philosophical system, he was very largely influenced by anatomical investigations. Even vivisection was employed by him, since his conception of lower animals as soulless automata opposed no scruples to such studies, however repugnant to popular feeling or condemned by his church. He was wont to point to the animals he had dissected, saying, "here are my books." Science he compared to a tree; metaphysics being the root, physics the trunk, and the most important branches mechanics, medicine, and morals; nor is it difficult to trace the effects of this conception in his treatment of the body.

Proceeding upon Harvey's discovery of the mechanics of circulation, he taught that the friction involved in circulation sufficed to vaporize and excite various elements in the blood. Some of these elements pass to the reproductive organs and behave as the forerunners of Darwin's gemmules might be

expected to, while others, destined to the brain, there evolve the gaseous "animal spirits" on which nervous action depends. So far as was necessary for his purposes, all ambiguities were cleared away and the relations between the unextended individual soul and the interblending currents of animal spirits as they entered or issued from the brain were dogmatically settled in a way refreshing to ears accustomed to the guarded statements of modern observers. It should be remembered, however, that his statements rested upon no inconsiderable amount of medical and philosophical authority.

That the notion that the soul, being unextended and a unit in our consciousness, must sustain a definite relation with the body at a single point, can be ascribed to Descartes, as implied by Wundt, is unwarranted, yet he did extend its currency so that even to-day, in a more or less obscure way, it burdens all psychological speculation.

Mechanical as were the doctrines of Descartes, he never went to the lengths of modern materialism in identifying physical and psychical. He did not identify the "vital spirits" or their interplay with the soul life.

All nerves are tubes containing these spirits, and in sensory nerves the agitation passes toward the brain, where in the ventricles it is communicated to the central mass of vital fluid therein. The currents thus produced may, under suitable conditions, pass out through motor nerves to the appropriate muscles, producing what have since been termed reflexes.

The soul itself is lodged in the pineal body, which must be its specific seat; because, first, it is centrally located; second, it is the only unpaired organ of the brain; third, it is in direct communication with the ventricles.

The soul is usually affected by the currents setting from the body and fabricates its presentations from the impressions thus derived, but it also impresses its own acts upon the "vital fluids" giving rise to motor currents. Aimless eddys



in this fluid may issue in phantasy while there is a separate spiritual activity to correspond to each form of motion of the vital spirits. Emotions, for example, are the result of currents from the heart.

In a sense the soul is, as Wundt says, superfluous in this theory, and Descartes evidently is led to postulate its existence to account for the unity of consciousness. He accounts it an unnecessary luxury for lower animals which accordingly are automata, with only the illuſiory appearance of consciousness. It was a step easily taken by the French metaphysicians, a few years later, to apply the same principle to man and eliminate the psychical element entirely.

Under the influence of the German metaphysicians of the school of Wolff, for whom classification and analysis passed for explanation, there followed a revival of a tendency which had been frequently exhibited before to assign to various organs the mental processes separated by their analysis.

That the brain is associated with thought was recognized very early, and this view prevailed among the Greek physicians in spite of the fact that Aristotle described the brain as the most bloodless and inert organ of the body, designed to regulate the temperature of the latter, much as the condensing vapors of the sky mitigate summer heat and drought. Pythagoras, Hippocrates, and Plato clearly recognized the head as the seat of the intellect and will.

In the days of Ptolemy Soter, some attempt was made to localize functions; Erasistratus believed that the sensory nerves spring from the meninges, while the motor are derived from the substance of the brain itself, and Herophilus is said to have anticipated Descartes in teaching that the vital forces reside in the ventricles. The followers of Galen subscribed to the same view.

The Arabian physicians extended the doctrine of localization. Albertus Magnus assigned judgment to the frontal, imagination to the parietal, and memory to the occipital portions of the brain. The notion of animal spirits within the

ventricles survived to some extent until the eighteenth century. Malpighi was the first to ascribe the higher functions to the gray matter.

Now, to return to the period following Descartes, we find the rudiments of the theory of localization rapidly developing. Willis located memory and the will in the convolutions. Imagination was situated in the corpus callosum, sense perception in the striatum, sight in the thalamus, and involuntary acts in the cerebellum. Lancási placed sense perception in the callosum, while others located memory there. Meyer considered the cerebellum as the organ of abstraction and located memory at the roots of the cranial nerves.

Thus the way was prepared for Gall and Spurzheim. Though phrenology is primarily a system of psychology rather than of physiology, its hold upon the mind of the people is largely due to the purely empirical form in which it was clothed. Those who were incompetent to discuss the propriety of dividing all mental manifestations into twenty-six or forty-three faculties fancied it a matter of mere observation to determine whether special development of various regions of the head coincided with great preponderance of such faculties.

Gall's theory was based on the fallacious belief that the skull depends for its form on the growing brain, and therefore, its surface is a reflex of the development of the brain, and that the size and configuration alone determine mental power.

What really gave phrenology its popular power was the fact that it served to give a scientific character to certain theories which survived astrology under the name physiognomy or chiromantia. When deprived of other methods of anticipating the future, the people eagerly grasped at what promised to be an indirect method of accomplishing the same thing. Many of the principles utilized by these sciences are to-day recognized, as the effect of the environment upon the body, the effect of habit on the mind, the effect of the mind

upon the body, the laws of heredity, and the effect of acquired characters and environs of the parent upon the offspring. It is doubtless to the more or less skillful (often unconscious) utilization of the elements of truth contained in these principles that the apparent success of phrenology is to be ascribed.

So important did the practice of physiognomy become, that in the time of George II. Parliament passed an act condemning all persons pretending to skill in physiognomy as rogues and vagabonds and rendering them liable to public whipping and detention in the house of correction. Yet phrenology, with less of fact and no less of danger, claimed the adherence of no less a thinker than Comte, and Gall was given a nitch in the temple of Fame in close proximity to the critical philosopher.

While the appeal to nature has produced good results, and Gall's efforts have led to such works as Bell's *Anatomy of Expression* and have prepared the public for better things, it may be that they have long hindered scientific investigation in this fascinating field and account for the fact, that aside from Charles Darwin almost no capable observer has ventured to discuss the physiology of expression.

While Florens must be honored as the pathfinder in the experimental aspect of neurology, it must be remembered that although he recognized the cerebrum as the seat of the will and perception, he did not admit any direct relation to voluntary motions and sensations, but supposed the cerebrum to act as a whole, every part participating in every function with which the organ was endowed.<sup>(1)</sup>

Lorry, in 1760, had also suggested the non-participation of the cerebrum in functions of sensation and motion. This view, which was readily accepted as agreeing with psychological preconceptions, closed this field to investigation for upwards of fifty years.

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1 FLORENS. "Recherches expérim. sur les propriétés et les fonctions du système nerveux." 1824-1842.

The attempts which the more inquisitive or venturesome students made to awaken activities of the cerebrum by electric stimulation proving ineffectual, the whole territory of the cerebrum was abandoned until a fortunate accident during the Franco-Prussian war gave the impetus to observation and research. While operating upon a wounded brain, Fritsch had occasion to apply the galvanic current and was astonished to observe twitching of certain groups of muscles. The close of the war afforded Fritsch and Hitzig opportunity to apply the suggestion and experimentally verify the conclusions reached.

It was soon seen that the opening or closing of the current constituted the necessary stimulus, and that an intermittent current might be employed in the irritation of various parts of the cortex, with the result of invariably producing localized muscular contractions in some regions and awakening no reaction in others. These investigators openly avowed their belief that all psychical functions which owe their origin to excitement of the nerves or produce such excitation have localized areas upon the cerebral cortex.

The next step naturally was the verification of these suggestions by the removal of those areas to which the various functions were attributed. But extirpation did not at once perform what was expected of it. Its results were often ambiguous. Hitzig observed as a result of extirpation, loss of muscular sense or recollection of previous motions.

Carville and Duret<sup>(1)</sup> applied the term "paralysie de la motricité volontaire corticale" to this disturbance of function which by some observers was considered as loss of sensation. So Nothnagel<sup>(2)</sup> and Schiff.

Nothnagel called attention to the fact that the loss was sooner or later made good, and a gradual restoration of function followed. He believed that this fact militated against the belief in exact cerebral localization.

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1 Arch. de Physiologie norm. et pathol. 1875.

2 Virchow's Archiv, Bd. 57, 1873.



Various suggestions were offered; some supposing that the corresponding area of the opposite hemisphere might acquire the function of the lost portion, others that any other part of the same hemisphere might substitute for it.

In 1876 appeared Ferrier's *Functions of the Brain* which, however applicable the criticism of Munk may be ("roh war operirt, roh beobachtet, roh geschlossen") served to awaken interest and collected a large body of facts for subsequent analysis. From twenty-four experiments or so he was able to lay off the entire cerebrum into areas whose functions were defined in no ambiguous or doubtful manner—in strong contrast to the methods of German investigators.

Hitzig entered this field about the same time, but was unable to escape from the contradictions presented by his experiments.

Goltz brought to his aid a new method of investigation, which was expected to control the hemorrhage which interfered with extensive extirpation. The brain substance was removed by jets of water. His observations<sup>(1)</sup> led him to believe that injury to any part of the cortex produced disturbance of all the sensory and motor functions, which disturbances were roughly proportional to amount of injury. In most cases the disturbances were temporary and were considered due to inhibitory action of the injured part. He recognized that in some cases there was actual and permanent loss.

Prominent among those who have contributed permanent materials to the doctrine of cerebral localization is Hermann Munk, whose papers appeared in various periodicals from 1877 to the present time and bear evidence of unlimited patience and critical acumen. The first of these papers<sup>(2)</sup> contains a resumé of results obtained by extirpating circular cortical areas fifteen mm. in diameter and two mm. thick over the exposed portions of the brain. He concluded that a

1 GOLTZ, *Pflüger's Archiv*, Bd. 13-14.

2 *Verhandlungen der Physiologischen Gesellschaft zu Berlin*, 1876-77, No. 16.



line drawn perpendicularly to the longitudinal fissure from the sylvian fissure over the dorsal cortex limits a cephalic motor from a caudal sensory region, and marked out the now famous areas constituting the recollection centres of sight and hearing, laying much stress upon the fact that there is a gradual restoration of function in the case of vision. The restitution, instead of being due to a vicarious substitution of the corresponding organ of the opposite side, he ascribed to an acquisition of new vestiges by uninjured adjacent areas of the same hemisphere. The discrimination of disturbances of hearing made necessary simultaneous extirpation on both sides, an operation too severe to permit long subsequent observation for the determination of the period of restoration, if such exists.

The second paper<sup>(1)</sup> covers experiments upon atrophy or failure to develop in the cortical areas previously located in the case of puppies deprived of organs of vision and hearing. The experiments were carried on in duplicate with animals of the same litter and with ample control, giving results seeming to show that early loss of the eye produces slight but noticeable limitation in the development of the occipital region, etc. These results stand in opposition to those of Gudden, and the author admits that the macroscopic changes are on the whole insignificant, though sufficient in some cases to produce thickening or other modifications in the skull.

The third communication extends the investigation to include the monkeys, the results agreeing with those derived from the dog, except that in the monkey total extirpation of the visual region produces hemiopia, in other words, the visual fields of the two eyes overlap and optic fibres are distributed accordingly. Moreover, he was able to locate with more or less certainty the centres of general sensation within the motor areas. So complete a coincidence between the

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<sup>1</sup> Berliner klin. Wochenschrift, No. 35.

sensory and motor areas for special groups of muscles seemed, to say the least, remarkable, and in the view of the rather limited and cursory details given by Munk, it is not surprising that other investigators were somewhat incredulous.<sup>(1)</sup>

In closing the article, Munk offers a suggestion or two upon our topic, not without interest. Sensations of innervation which accompany motion are of greatest importance in assisting in the formation of concepts of motions of the body. From such innervation sensations the primary concepts of motor acts are derived in the young, and in case of loss of such concepts of motor acts in the adult by injury to the specific centres, they may be recreated from the reflex motions.

While it may be very convenient to predicate volition and voluntary motion as functions of the cortex, there is no observational basis for such a localization. We simply know that the cortex is the seat of perception and conception, and we are only justified in assuming with Meynert that concepts of motion are the causes of so-called voluntary motions; that when such concepts arise from association, the motion follows *eo ipso*, unless in some way inhibited; and that the motion is the more extensive the greater the concept of motion producing it. The perception of the intensity of will in voluntary motion is an attribute of a concept of motion.

Those familiar with the recent literature of physiological psychology will observe that these statements are somewhat at variance with those of Wundt, etc.

In the fourth contribution<sup>(2)</sup> new evidence is added to the same effect. The whole available surface of the cerebrum was found to contain sensory centres, even the frontal region, usually relegated to higher faculties, not excepted. Instead of psycho-motor and psycho-sensory centres there are only sensory areas. The cortex has only to do with perceptions

<sup>1</sup> See supra p. 99.

<sup>2</sup> Verhand. der Physiolog. Gesellsch. zu Berlin, 1878-79, Nr. 4, 5.

and concepts which may issue in motions. In response to the question: "Where then, is the seat of the intellect?" Munk replies, "The intellect has its seat over the entire cortex, for it is but the sum and result of all the concepts arising from sense-perceptions. Every lesion of the cortex impairs the intelligence, the injury increasing with the extent of the lesion."

The fifth contribution is chiefly of interest because of the attempt to determine areas of the occipital cortex corresponding to all parts of the retina, and the discussion of causes of partial decussation of optic fibres in animals whose visual fields are not mutually exclusive.

In the seventh of these papers we need only notice the single case recorded of a bilateral disease of the hippocampus which resulted, in all appearance, in complete loss of the sense of smell, an observation which derives some value from the fact that the hippocampus is about the only region which has not been experimentally investigated, and smell and taste and smell are the only specific sensory functions not localized.

At a time when Munk's views seemed to enjoy an easy triumph, there appeared an article by Loeb<sup>(1)</sup> which contained results, which, if reliable, would have undermined all the work of Munk and his Italian collaborators, Luciani and Tamburini, not to mention Ferrier.

He concludes, "I have never observed a motor disturbance after lesions of the occipital lobe without injury to vision or disturbance of vision, after lesions of the parietal lobe without motor disturbance. On the other hand, visual disturbance was frequently encountered alone on injury to the occipital lobe." Injury to any part of the cortex might produce visual disturbance. In short, we cannot tell whether the cortex contains a specific apparatus for visual perception or not.

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<sup>1</sup> LOEB, "Die Störungen nach Verletzung der Grosshirnrinde," *Pflüger's Archiv*, XXXIV. 1884.

In 1885 there appeared a work bearing the names of Luciani and Seppilli, already familiar to specialists by reason of numerous smaller works, which may long serve as a *vade mecum* for experimenter in this domain. Although almost immediately translated into German<sup>(1)</sup> this work is almost unknown in this country.

The unwarrantable assumptions of Goltz, which demand positive inhibitory reactions from the injured areas in explanation of the restitution of function, and the great diversity in the use of terms led these authors to an analysis of the available methods for determining cortical functions from extirpation, which it may not be useless to repeat. These methods are as follows:

1. Negative results of extirpation. We may safely and confidently assume that functions not disturbed by the lesion have nothing to do with the area removed.

2. Comparison of positive effects of extirpation of homologous parts. This method suffers from the impossibility of distinguishing the effects of removal of a given area from the accessory disturbance due to the irritation and circulatory disturbances, especially the septic after-effects. The comparison is also rendered difficult by the variability of the cortical topography even in the same species or sides of the same brain.

3. Comparison of effects of extirpation of different areas of the cortex. This method is of especial value in determining the extent of the collateral effects, and indicates as a rule that the collateral disturbances usually include functions closely allied to those directly involved in the injury.

4. Comparison of effects of successive extirpation in the same animal. This method is especially available in the investigation of compensating areas.

5. Determination of the minimum extirpation producing

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<sup>1</sup> LUCIANI UND SEPPILLI, "Die Functions-Localization auf der Grosshirnrinde an Thierexperimenten und klinischen Fällen nachgewiesen." (German by Fraenkel). Leipzig, 1886.

a given physiological effect. This method serves to define the limits of special centres.

A useful criticism of methods of determining the nature and extent of functional (sensory) disturbance follows.

Of the conclusions growing out of the extended and detailed researches of these authors, the following resumé must suffice.

Both schools of experimenters are partly right and partly wrong. Localization is not possible in the arbitrary way attempted by Munk, neither can it be denied so abruptly as by Goltz. There are areas corresponding to the several classes of sensations, but these cortical areas overlap to a very great extent, so that injury to any part of the cortex may induce disturbances of a large number of functions. There is an inner nucleus or sphere for each sense, however, and these are located much as indicated by Munk.

Extensive cortical lesions produce changes in disposition because of the loss of the normal association of percepts and images in the soul. Of the two views, 1st, that the cortex contains centres for all mental manifestations, even to the crudest sensations and motor impulses; and 2d, that the cortex is solely concerned with concepts derived from the several senses and voluntary impulses as well as memory and attention, the authors seem to lean to the latter. The corpus striatum is regarded as an integral part of the cortex as much as the hippocampus.

The attempt of Munk to substantiate a topographical projection of the retinal areas upon the cortex is considered contrary to the facts brought out and summarily dismissed. On the other hand, it is concluded that the cortex contains only centres of sense-perception with their correlated memory-images, while simple sensation and motor impulses are located in the lower centres.

One apparent contradiction involved in the localization theory grows out of the phenomena associated with complete removal of the hemispheres. Goltz succeeded in extirpat-



ing both hemispheres of the dog and preserving the animal alive for fifty-one days after the operation. <sup>(1)</sup>There was a complete loss of special sensation, though dermal sensation was persistent and there was no muscular paralysis. A touch was sufficient to awaken it from its lethargy, and locomotor coördination was not destroyed. Goltz claims that this operation does not necessarily completely destroy vision. When food was introduced far enough back in the mouth, it was properly masticated and swallowed. Goltz concludes that the disturbances following extirpation are largely due to inhibition arising from degenerative changes in the tracts injured.

This view Wundt has used in an opposite way. After repeating the experiments of Goltz, with his usual careful analysis of technique, he concludes that many of the functions ascribed by Goltz to inferior centres, are due to irritative degeneration along the stumps of the severed nervous tracts. His own experiments, he thinks, prove conclusively that when such irritations are excluded, not only are the psychical functions entirely obliterated, but the illusory appearance of spontaneity and sensation disappear. Goltz's methods are regarded as crude and unreliable.

It would be unfair to neglect the older results of Christiani and Schrader. The former<sup>(2)</sup> removed both hemispheres of the rabbit and concluded that under those circumstances the animal retained the functions of vision and hearing as well as dermal sensation, though in a vague and feeble form.

A pigeon when deprived of the hemispheres seems to retain many of the functions usually ascribed to the cerebrum, and in lower animals it is still more difficult to determine any definite localization of functions.

The bearing of the progressive differentiation of cerebral localization upon psychical evolution will be discussed in the

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<sup>1</sup> *Pflüger's Archiv.* Bd. 42, 1888

<sup>2</sup> CHRISTIANA, *Für Physiologie des Gehirns*, 1885.

second part of this article. The writer has endeavored to show that consciousness in the limited sense is of comparatively late origin, and that a rigid application of the doctrine of natural selection would exclude it from all participation in nervous activities until such time as the struggle for survival had become ameliorated to an extent, making conscious selection possible without involving direct loss or destruction. After such a field for spontaneity had been opened, consciousness would become a valuable and then a necessary adjunct, and the effect of the reaction of conscious beings upon each other would be to widen the arena for its display and increase the complexity of its activities.<sup>(1)</sup>

Passing over the valuable evidence derived from human pathology and so ably analyzed by Nothnagel and Naunyn<sup>(2)</sup> and the digest of recent efforts in this direction given in *Brain* during 1889 by C. K. Mills, we may examine, for a moment the bearing of the most recent histological work. A paper by Koelliker,<sup>(3)</sup> which appeared in December, 1890, is occupied chiefly with the application of Golgi's method to the study of the spinal cord. The positive anatomical results may be summarized as follows:

1. Sensory fibres on entering the cord divide into an ascending and descending limb, which pass through the dorsal column and lie on the surface of the substantia gelatinosa.

2. No connection of the dorsal root fibres with nerve cells has so far been observed.

3. The fibres of the longitudinal dorsal tracts give rise to lateral branches (collaterals), which enter the gray substance, terminating in free stumps which are especially abundant in the marginal zones of the substantia gelatinosa and Clarke's columns.

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<sup>1</sup> This subject was discussed in a lecture before the University of Cincinnati, April, 1891, a synopsis of which will be incorporated beyond.

<sup>2</sup> Verhand. des VI Congresses f. innere Medicin zu Wiesbaden, 1887.

<sup>3</sup> "Zur feineren Anatomie des centralen Nervensystems" Zeitschrift f. wiss. Zoologie, Bd. LI, p. 1.

4. Motor root fibres arise from large and small nerve cells in all parts of the ventral cornua, each by a single nervous process.

5. The ventral and lateral columns consist in part of fibres from all regions of the cord.

6. The greater number of longitudinal fibres of the ventral and lateral columns give rise to lateral branches (collaterals), which enter the gray matter, especially of the ventral cornua and ventral part of the dorsal cornua.

7. All collaterals of lateral columns and nervous branches of cellular processes, as well as the inflexed termini of sensory nerves, give rise to a larger or smaller number of branches, each finally form fine brushes of fibres, which collect about nerve cells without coming into actual connection with them or anastomosing with each other.

8. Nerve cells of the cord are, (*a*) motor cells, (*b*) cells of the columns, (*c*) cells of the dorsal cornua whose nervous processes do not extend beyond the gray matter, but subdivide uniformly.

Respecting the relation of cell and fibre, Koelliker concludes that interaction may follow two methods: 1st, direct stimulation of a fibre by a cell (motor); 2nd, operation of nerve fibres upon cells with which they are simply in contact but are not directly connected (sensory cells).

Voluntary motion is thus construed. Impulses conveyed through pyramidal fibres pass into collaterals whose fine branches are in close contact with cells of the ventral cornua from which motor nerves arise. The excitement is thus imparted to these cells, and is transmitted through the nerve fibres to the muscle. Koelliker considers that the motor cells are collected in niduli which correspond to the metameres of the body.

Sensations, on the other hand, are conveyed by the dorsal columns, but there is no evidence that they continue to the cerebrum. Data derived from ascending degeneration seem to indicate that these fibres end in the niduli of the medulla.

In this connection we may call attention to data derived from our study of the opossum, which have an indirect bearing on the above. In the ventro-caudal part of the cortex, *i. e.*, cortex beneath the rhinalis fissure, we were able to demonstrate the termination of the numerous elongate cells in a peripheral branch, which divides in the neuroglia layer to form just such a neuro-pilem as has been described by Golgi and Koelliker in the cord. Peripherad to this is a tract derived in part from the olfactory. It seems probable that there is over the entire sensory region at least such a continuous meshwork or felting of fibres which might be regarded as an anatomical basis for assuming a single organ of consciousness. A similar neuro-pilem is found as a result of the subdivision of the central (basi-lateral) processes of these cells, so that the cells do not pass into direct connection with axis cylinders in either direction. In motor cells we have traced axis cylinders to the fibrous meshwork connected with the lateral processes of the deeper pyramids, but suspect that the apical processes are connected with a neuro-pilem or nervous felting of a similar sort, but observation is here made enormously difficult by the mingling of sensory and motor cells which are sharply distinguished.

These questions will be discussed hereafter, as this review is already longer than was intended, so that the bearing of the neurological suggestions upon the question with which we set out must be deferred to a later article. It may be added, that if psychology really needed a material sensorium commune, or a common arena for consciousness, the suggestions which we now have of a neuro-pilem covering the entire cortex and containing the finely divided fibres of centripetal and centrifugal nerves which are merely closely associated without anastomosis, might seem to afford it without the necessity of setting aside the results of localization already given. If, on the other hand, we are justified in accepting the assurances of Wundt and Lotze that the concept of extension is out of place as applied to the soul,

we still require from the standpoint of physiology some common ground for interaction, such as would be furnished by the nerve-felt of the cortex. See in this connection the discussion of the cortex in the article upon the "Anatomy of the Brain of the Opossum," *supra*.<sup>(1)</sup>

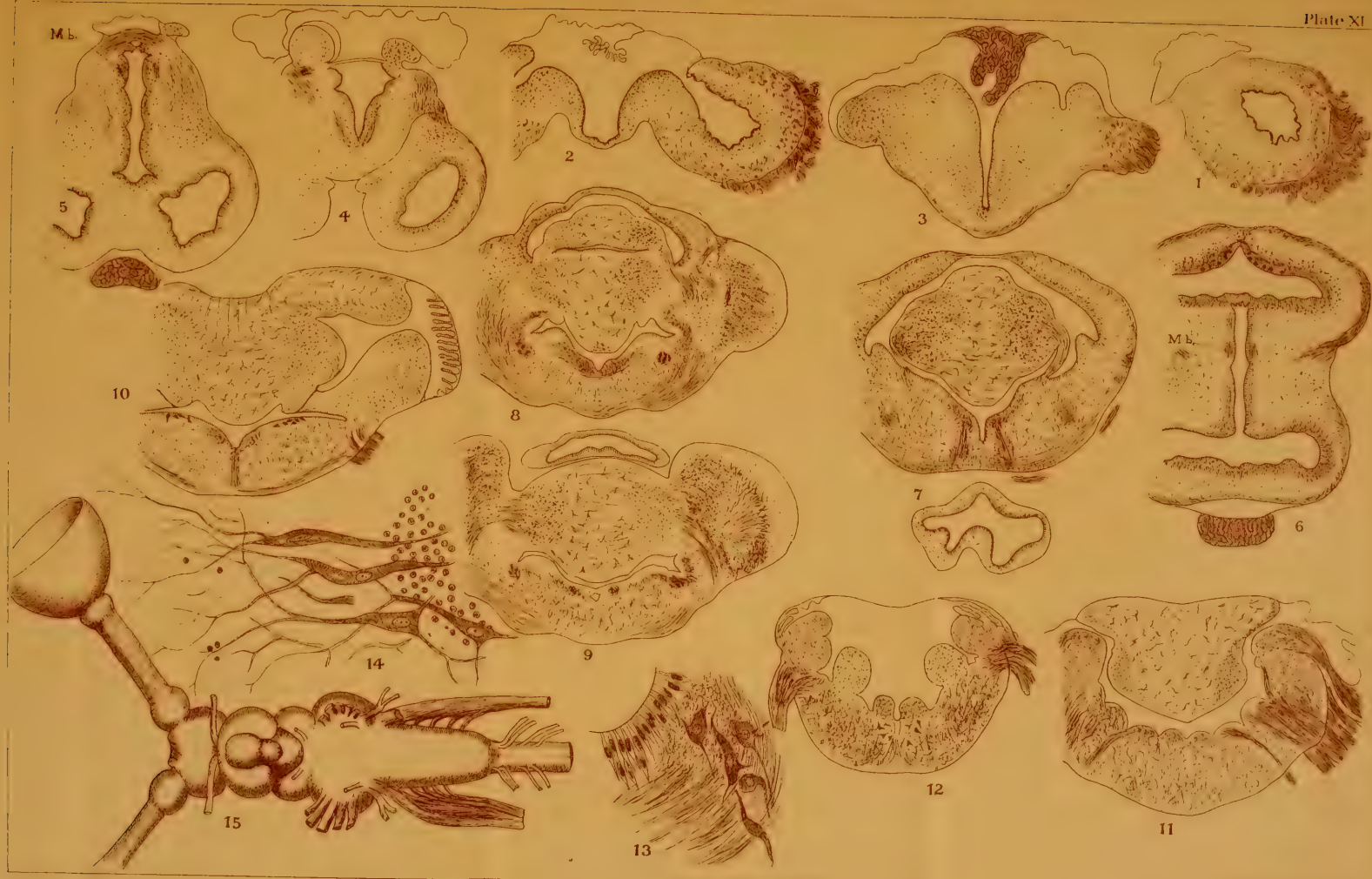
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<sup>1</sup> Since the above was written we have received the "Report of Six Lectures on Cerebral Localization," by DR. HENRY H. DONALDSON, *American Journal of Psychology*, IV, 1, p. 113.



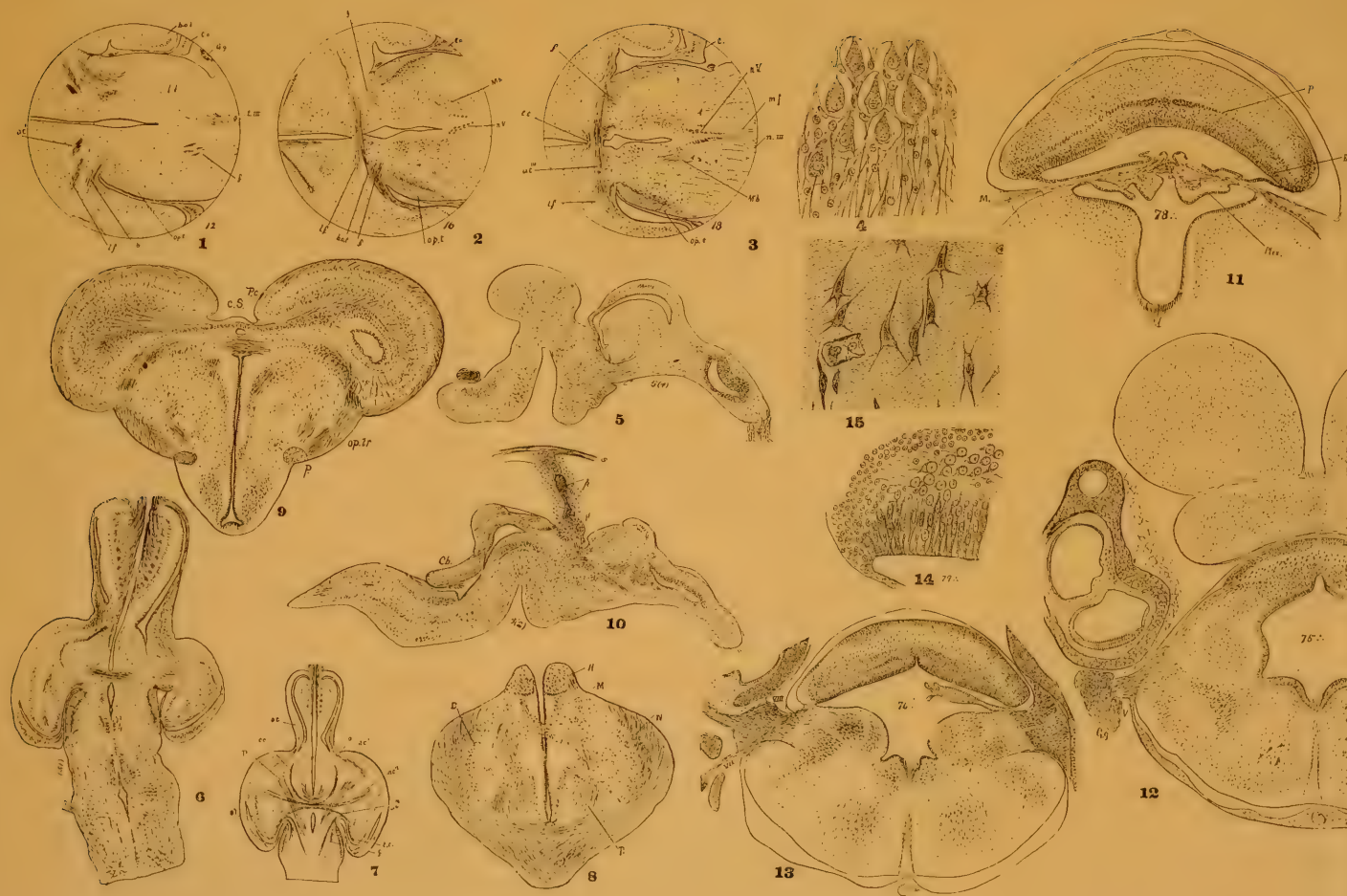










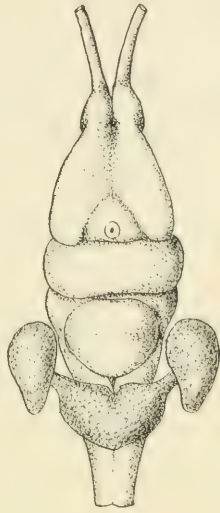




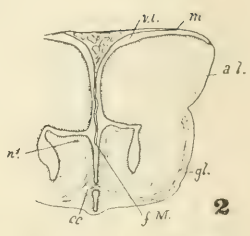




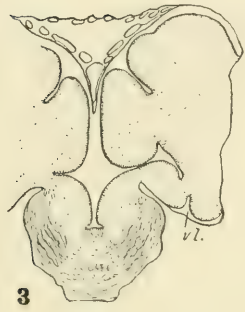
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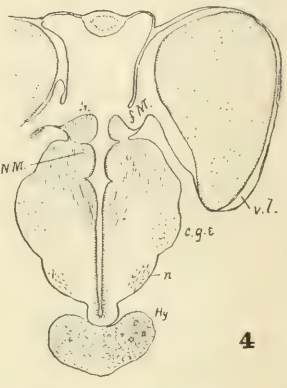
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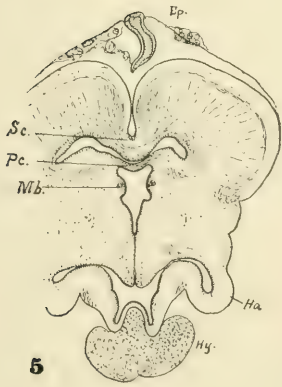
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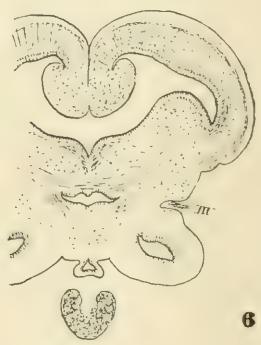
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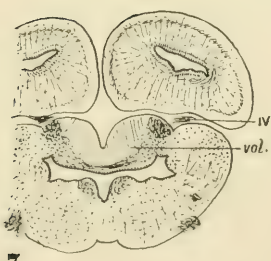
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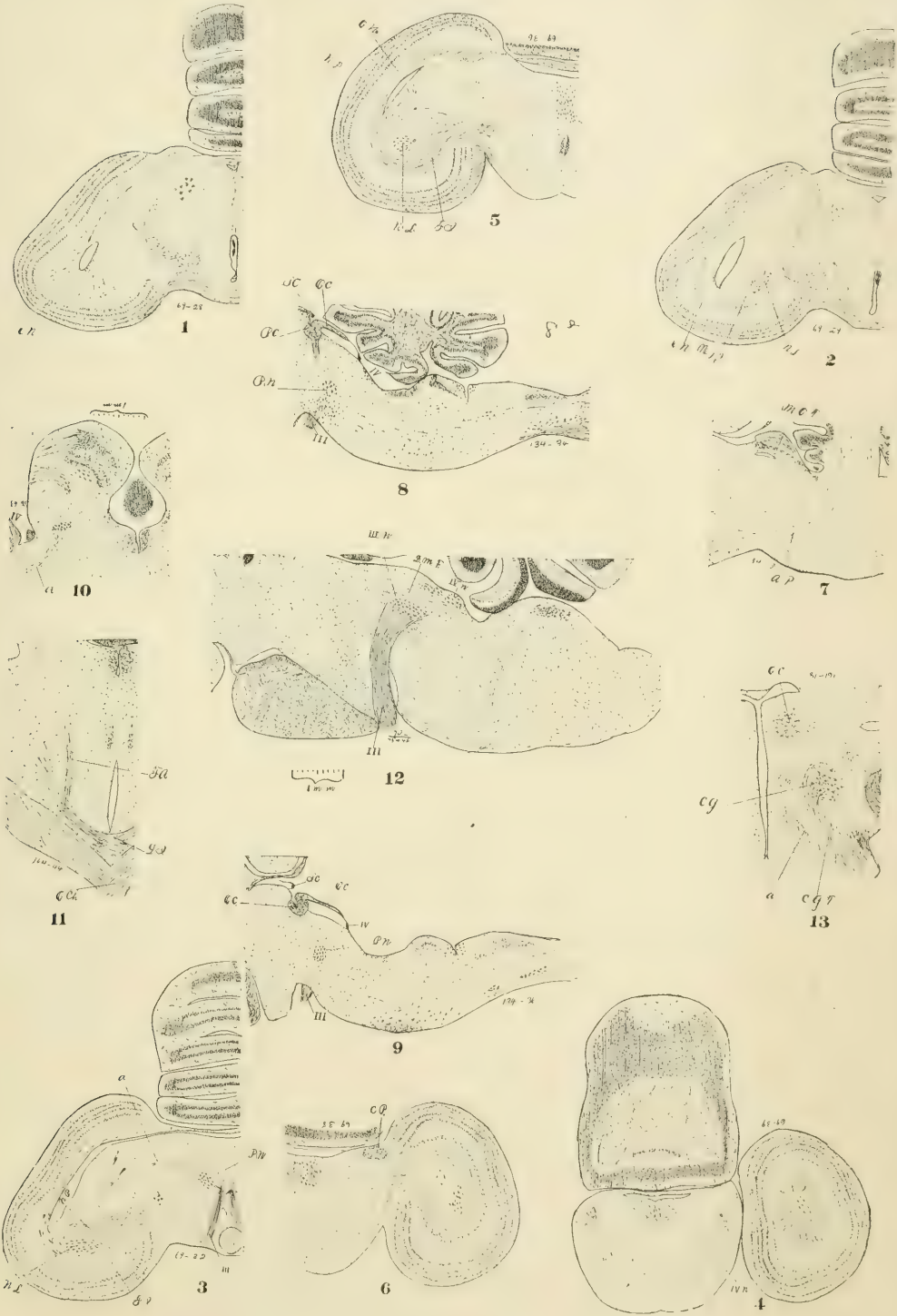


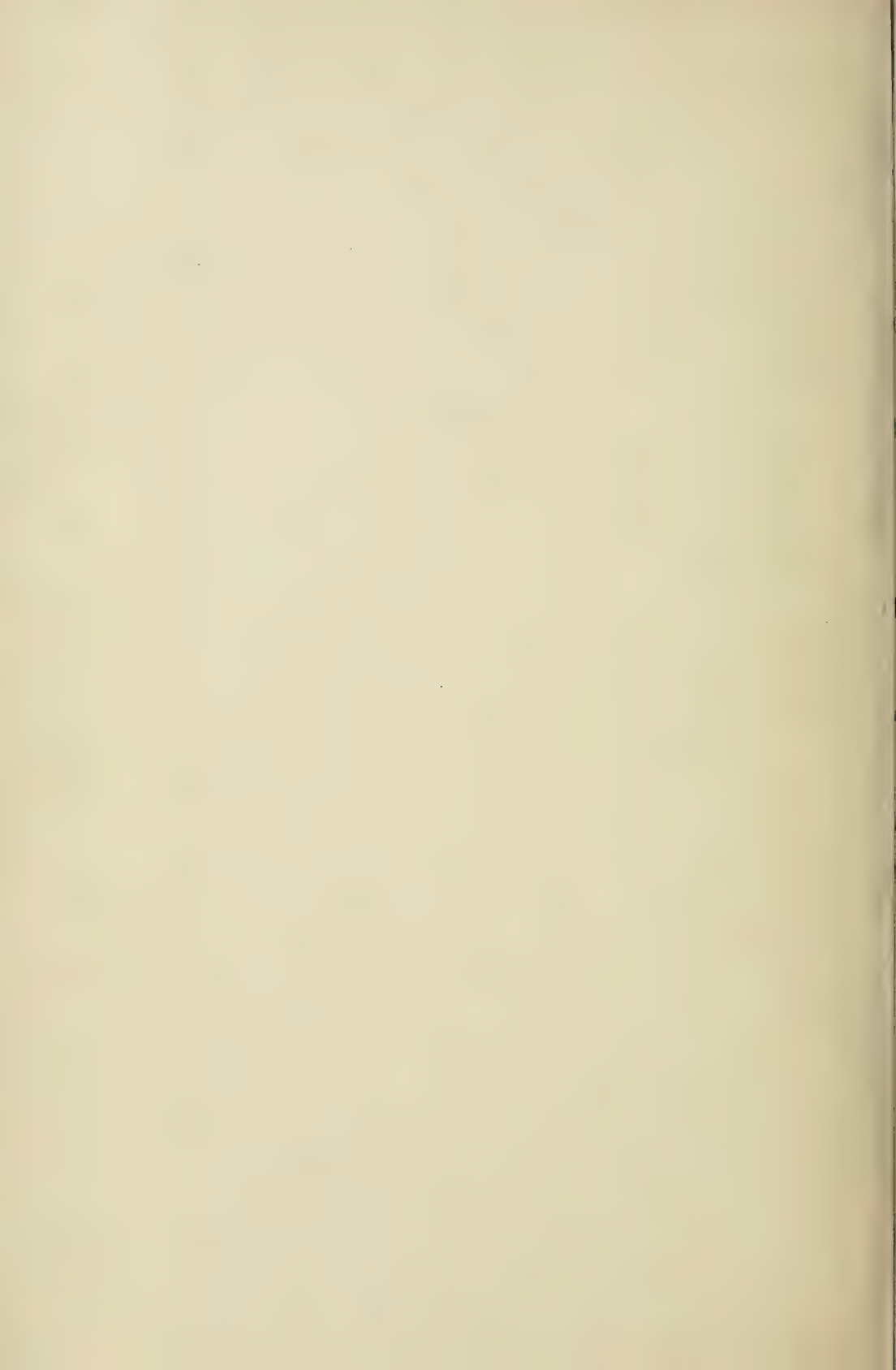
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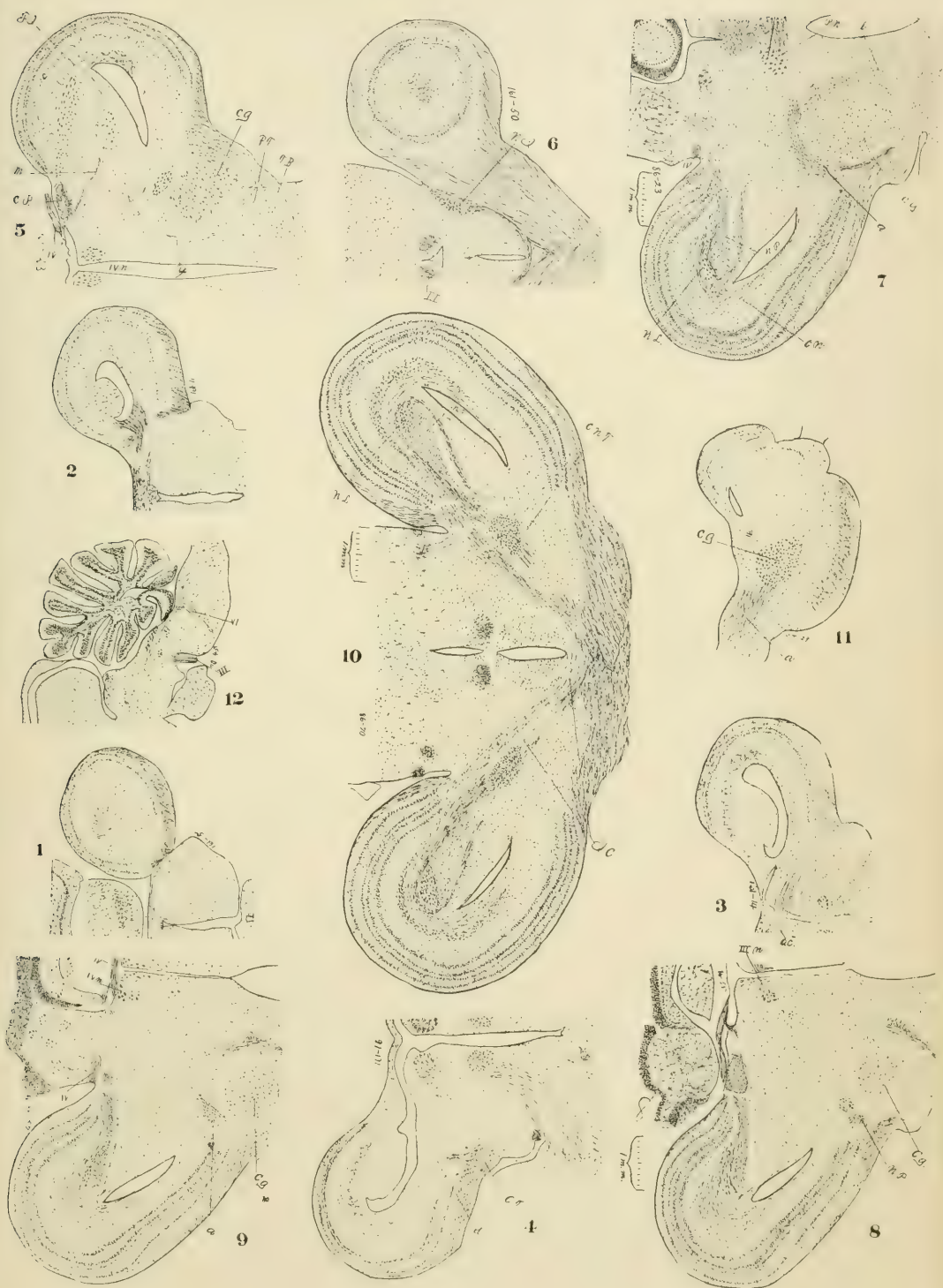
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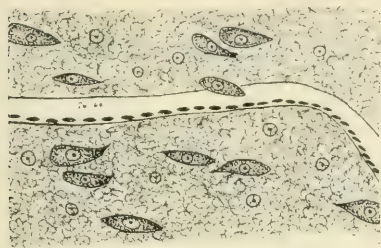




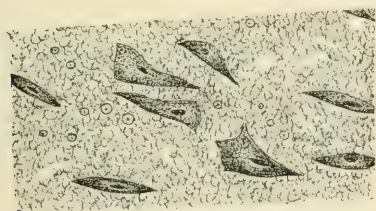




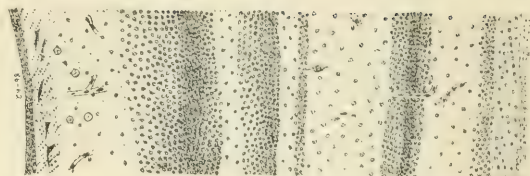




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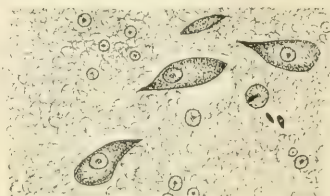
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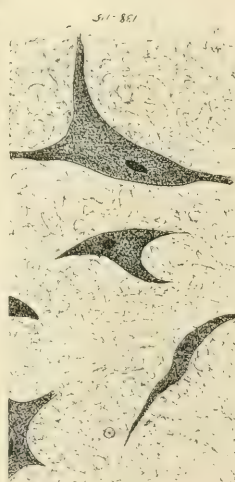
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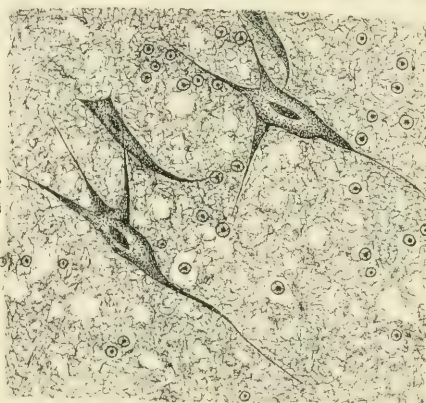
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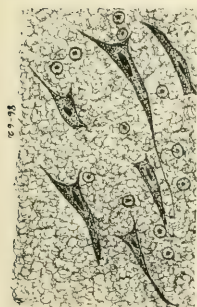
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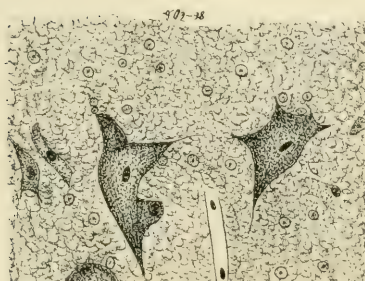
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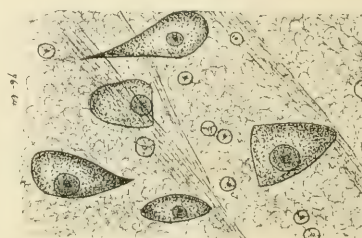
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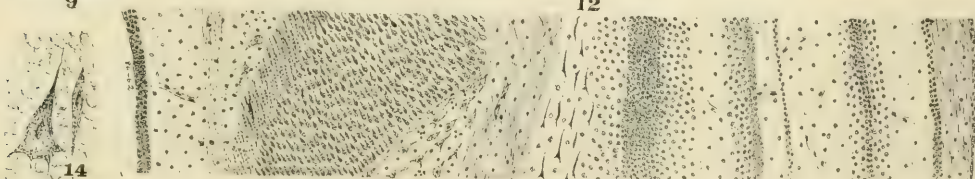
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THE MORPHOLOGICAL IMPORTANCE OF THE  
MEMBRANOUS OR OTHER THIN PORTIONS  
OF THE PARIETIES OF THE  
ENCEPHALIC CAVITIES.<sup>(1)</sup>

BURT G. WILDER, M.D.

Professor in Cornell University.

In the JOURNAL OF COMPARATIVE NEUROLOGY for June, 1891, p. 152, the editor, Prof. Herrick, in reviewing previous publications upon the brains of the ganoids and other fishes, ascribes my failure, in 1875, to recognize a certain homology to my not taking into account the existence of certain thin portions which are commonly removed in preparing the brain.

Upon the present occasion I offer no opinion upon the particular homologies in question; these and many others in the diversified brains of the fish-like vertebrates, I hope to reconsider hereafter. My object now is to acknowledge the justice of Prof. Herrick's criticism, and to add that for several years it has been my intention to publish a far more vigorous denunciation of the errors as to method and interpretation of which I was guilty fifteen years ago.

This would have been in accordance with the sentiment, long entertained but hitherto unexpressed, that, since every one makes mistakes, the interests of all concerned would be best subserved by the adoption of the custom of each correct-

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<sup>1</sup> Read at the meeting of the Association of American Anatomists, September, 24 1891.



ing his own, either as soon as discovered or periodically; a sort of scientific confession of sins.

The natural corollary to this would be that each well-disposed discoverer of another's fault would inform him privately so that he might make prompt correction. This plan I have followed in several cases, and have reason to believe it has served to avoid personal irritation and the needless repetition of criticism.

As to the particular matter to which Prof. Herrick has called attention, my procrastination has been due to several causes; one, the lack of time to review the whole subject, and another, the consciousness that, whenever it was done, there would have to be condemned not only my figures and descriptions but those of our morphological leaders, Agassiz, Gegenbaur, Huxley, Owen and Jeffries Wyman; for neither they nor any others, so far as I know, up to the publication of Rabl-Rückhard's papers in 1883 and 1884, seem to have perceived adequately the necessity of admitting the complete circumscription of the encephalic cavities with "fishes," and thus of recognizing the morphological significance of the thin, or even wholly membranous portions of the brain. This criticism, ungracious as it is, can be no longer deferred; to speak pathologically, the predisposition which has long been dormant in my mind has found in Prof. Herrick's kindly commentary an "exciting cause."

I may be permitted to add, in partial reparation for my own share in this grave morphological dereliction, that the need of considering the membranous portions of the mammalian brain was recognized as early as November, 1876;<sup>(1)</sup> that in several subsequent publications<sup>(2)</sup> the morphological

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1 My colleague, then fourth-year student, Prof. S. H. Gage, has preserved the notes of dissections of cats' brains, dated November 25, 1879, and January 1, 1877, made for the purpose of demonstrating the complete exclusion of the thalamus from the paracæle (lateral ventricle) by the membranes and plexus connecting the contiguous margins of the tænia and fimbria, and the point is made in the printed synopsis of a lecture to the class in Physiology in the former month.

2 "The Brain of the Cat," *Philos. Soc. Proc.*, 1881; "Anatomical Technology," 1882, 1886; "The Cartwright Lectures," 1884, *N. Y. Medical Journal*, XXXIX, pp. 142, 147,

significance of apparently atelic portions of the brain is insisted upon; that, in 1887 (*American Assoc. Proceedings*, 251, and *American Naturalist*, XXI, 913-917), I based a primary classification of animals upon the presence of a circumscribed cavity (neurocœle) in the central nervous system (neuraxis); that, since 1880, all vertebrate brains in the Museum of Cornell University have been prepared with special heed to these parts, and the method of alinjection or injection of alcohol has been generally employed; finally, that, in addition to the special students in the anatomical laboratories, there is no member of even my general classes in Physiology and Vertebrate Zoology who has not learned the meaning of the phrases *endymal continuity* and *calian circumscription*.

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#### METAMERISM OF THE VERTEBRATE HEAD.

If anything were necessary to convince one of the strong place the problem of the segmentation of the head has made for itself in all branches of morphology, it would be afforded by the large number of papers more or less directly concerned with it read at the last meeting of the Anatomical Society held in Munich during the present year.<sup>(1)</sup>

The paper by Zimmermann quoted is devoted to a discussion of the segmentation of the brain, and the conclusions may be summarized as follows:

In an early stage there appear in Salamander on either side of the medullary tube and in front of the first provertebra-rudiment eight similar dilations. In higher verte-

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179, 654, etc.; "The Relation of the Thalamus to the Paracœle," *Journal of Nervous and Mental Diseases*, July, 1889; and the articles in the "Reference Handbook of the Medical Sciences," Vol. III, 1889

1 C. VON KUPFFER, "Die Entwicklung der Kopfnerven der Vertebraten."

FRORIEP, "Zur Entwicklungsgeschichte der Kopfnerven."

KILLIAL, "Zur Metamerie des Selachierkopfes."

ZIMMERMANN, "Ueber die Metamerie der Wirbelthierkopfes."

GAUPP, "Zur Kenntniss des Primordial-Craniums der Amphibien und Reptilien."

brates the three cephalad encephalomeres are much larger. These subsequently divide, the primitive prosencephalic vesicle into two, the mesencephalic and the third each into three. The author thinks the three first are originally compound, and that for some reason the subdivision is retarded in this region. The thirteen encephalomeres are therefore homologous. These are especially prominent in *Mustelus* and *Acanthus* (Selachii).

The first encephalomere forms the secondary prosencephalon, with only a dorsal nerve root represented by the olfactory. The second forms the thalamus, and is devoid of nerve roots. The third, or first mesencephalic encephalomere, is also devoid of nerves. The fourth bears the ciliaris as a dorsal and the oculo-motor as a ventral root. The seventh is doubtfully credited with the trochlearis. The eighth has the sensory root of the trigeminus as its dorsal and the motor trigeminus as its lateral root. The ninth has no nerves. The tenth with the profacialis (sensory part + acoustic) as a dorsal root and a lateral root. The eleventh bears the acoustic ganglion as dorsal root, a lateral branch entering the genu of the facialis, and the abducens. The twelfth bears the sensory glosso-pharyngeal, a lateral branch, and a ventral branch which passes dorsad behind the glosso-pharyngeal. The thirteenth also has three roots, the sensory fibres of the tenth, a lateral branch chiefly in the accessory, and a ventral branch passing dorsad behind the vagus.

The four following neuromeres enter the skull in mammals and have dorsal roots in the vagus, lateral ones in the accessory, and ventral ones in the hypoglossus.

The vagus of mammals includes five dorsal roots. Prof. Froriep remarks that he has detected two neuromeres in the diencephalon. This latter statement the present writer is able to substantiate from his own observations on *Cavia* and *Canis* embryos, though very doubtful as to the homology of these segments with the neuromeres of the spinal regions.  
—[Ed.]

## THE ARACHNOID OF THE BRAIN.<sup>(1)</sup>

F. W. LANGDON, M.D.,

Professor of Surgical Anatomy in Miami Medical College, Cincinnati.

### 1. *Its General Homology with the Serous Membranes of the Other Great Cavities.*

Modern works on human anatomy do not give, as a rule, an account of the cerebro-spinal arachnoid, which is, in the opinion of the writer, in harmony with its structure, topography, and relations as shown by dissection.

Some of the different views which have existed respecting the subject, as well as the present consensus of opinion of our commonly accepted authorities, are exhibited in the following historical notes:

According to Bichat,<sup>(2)</sup> "in the middle of the seventeenth century it began to be suspected that . . . the arachnoid and pia . . . might possess a separate existence." "The Anatomical Society of Amsterdam assured themselves of the fact in 1665; Van Horne soon after demonstrated the arachnoides separately to his pupils."

Bichat himself <sup>(3)</sup> describes the arachnoid as a serous shut sac, conforming in all essential particulars with the serous membranes of the other cavities. This was apparently the

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1 Read before the Association of American Anatomists at the annual meeting, Boston, December 29, 1890, and reprinted from the N. Y. Medical Record, August 15, 1891.

2 XAVIER BICHAT, etc., "A Treatise on the Membranes in General, and on Different Membranes in Particular," Paris, 1802. Translated by John G. Coffin, M.D. Boston, 1813, p. 163.

3 Op. cit.

generally accepted view up to the time of Kölliker, who wrote:<sup>(4)</sup> "It is generally stated that the inner surface of the dura mater is covered by an outer layer of the arachnoid; but nothing is found here excepting an epithelium composed of polygonal cells, and there is not a trace of a special membrane."

The same writer (page 238), speaking of the spinal membranes, says: "The inner surface of the dura mater is covered with a multiple layer of pavement epithelium cells, but has no other investment which could be regarded as a parietal lamina of the arachnoid." Again, Frey<sup>(5)</sup> says: "The arachnoid, which has also been numbered among these (the serous membranes), has no parietal layer." And, "The second membrane, the arachnoidea, was formerly described as forming a shut serous sac, but erroneously so; the parietal leaf being usually represented as fused together with the outer layer of the dura mater, since it could not be demonstrated separately."<sup>(6)</sup>

Without multiplying references unnecessarily, it is sufficient to state further that in the various editions of Gray's "Anatomy," previous to 1870, the arachnoid is described as a shut sac. Darling and Ranney, 1882, also teach this view; while Gray (after 1870), Holden, fifth edition, 1885; Leidy, 1889; Weisse, 1886, and other leading works in common use as text-books, speak of it as consisting of one layer only—the "visceral" layer.

It has occurred to the writer that this question of one or two layers was one which it was desirable to have settled, and if possible by macroscopic rather than microscopic evidence. With this object in view a series of dissections were made as follows:

First dissection: Fœtus at term, still-born.—The scalp being removed, a section of skull was made in the parietal

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4 "Manual of Human Microscopic Anatomy," p. 237-238. London, 1860.

5 "Histology and Histo-chemistry of Man," p. 227. Appleton, 1875.

6 Op. cit., p. 599.



region, removing the bone only. The following features were then easily demonstrated in successive order: 1. Periosteal layer of dura, traceable to its continuity with the sutural "ligament." 2. The dura proper (subserous connective tissue), forming the walls of sinuses and carrying the nutrient vessels for, 3. The parietal layer of arachnoid, a thin pellicle separable with the handle of the scalpel. 4. Space between parietal and visceral layers of arachnoid, or the arachnoid cavity proper. 5. Visceral layer of arachnoid passing over sulci, etc. 6. Subarachnoid space. 7. The pia mater. 8. The convolutions.

Second dissection: Fœtus at term.—This was practically a repetition of the first, except as to region, the frontal bone being removed instead of the parietal.

Third dissection: Adult, negro, aged about thirty-five, brain and membranes normal.—The dura covering vertex and forming falx cerebri and tentorium was found to be inseparably united with the parietal arachnoid; at the base of the skull, however, and especially in the region of the sella turcica and orbital plates, the two membranes are quite freely separable with an ordinary scalpel, and the arachnoid could be stripped off in places. This separation also was more marked at the points of exit of the larger cranial nerves—*e.g.*, the optic. The following diagram (*A*) will show at a glance these points in the parietal region of the newborn infant—the only change in adult life being fusion of the vertical parietal arachnoid with the subserous dura, a condition in every way similar to the conditions which exist in the pericardium. At the base of the skull, however, the separation is readily appreciable in the adult, as already stated.

Considering the nature of the sinuses—as simply dilated veins—and the fact that the inner dura is the necessary medium for vascular supply of the parietal arachnoid, it would seem in every point of view proper to consider the inner dura as homologous with the subserous connective tissues elsewhere.

The writer regrets that material and time have not permitted these observations to be carried to their logical conclusion, by actual sections of cranial nerve exits, to show the arachnoid reflections.

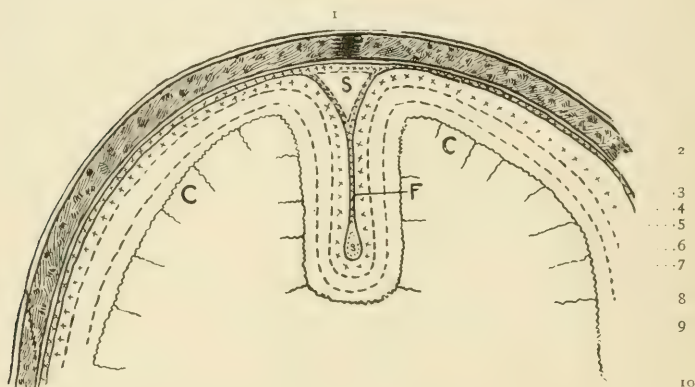


DIAGRAM A. Vertical Transverse Section of Parietal Region to Show the Various Membranes and their Layers.—1, Sutural "ligament," continuous with external periosteum and periosteal layer of dura; 2, parietal bone; 3, periosteal layer of dura; 4, inner layer of dura, forming sinuses; 5, subserous connective tissue, between dura and parietal arachnoid; 6, parietal arachnoid; 7, arachnoid cavity; 8, visceral arachnoid; 9, subarachnoid space; 10, pia mater; S, superior longitudinal sinus; s, inferior longitudinal sinus; F, falx; C, convolutions.

2. *The Communications between the Arachnoid Cavity and the Subarachnoid Space by Way of the "Lunulate Foramina."*

During the progress of the last dissection it was evident that there were two points at the base of the cranium where the arachnoid was deficient over a considerable area on either side of the medulla oblongata. These deficiencies present the form of bilateral foramina—one on each side—and are situated in the "bridge" of visceral arachnoid which stretches across from the cerebellar lobes to the under surface of the medulla. These foramina measure about half an inch in longitudinal diameter by one-fourth inch transversely, and are crossed by three or four fibrous bands, the attachment of

which to the edges of the openings produces a multiple crescentic appearance of their margins, which suggests the name adopted above. (See Diagram B.)

As the body had been subjected to but little handling before the autopsy, and the brain was removed with special care, it does not seem likely that these openings were produced accidentally; the finished appearance of their edges and close correspondence with each other in all respects would also negative this supposition.

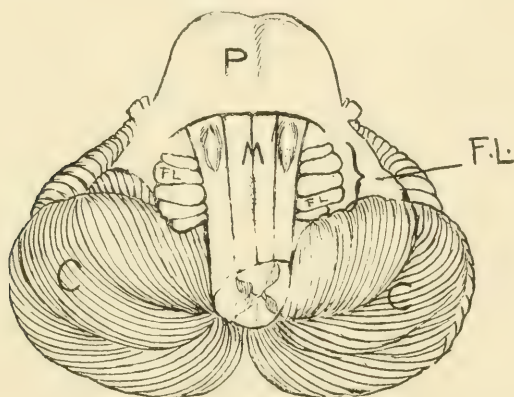


DIAGRAM B.—Lower or ventral surface of pons (P), medulla (M), and cerebellum (C), supposed to be covered by the viscera arachnoid, in which are seen the lunulate foramina (F. L.) in outline. NOTE.—The artist has failed to represent the membrane, but the outlines of the foramina are correctly placed.

It is evident that, if constant, they form a large and direct communication between the arachnoid cavity and the sub-arachnoid space and ventricles, just opposite the “foramen of Magendie”—by which the subarachnoid space is stated by most anatomists to communicate with the internal cavities.

Hence, it would seem reasonable to suppose that the cerebro-spinal fluid may have its origin, in large part at least, in the walls of the arachnoid cavity proper, reaching its final destination through the lunulate foramina to the sub-

arachnoid space, thence *via* the "foramen of Magendie" to the ventricles.

Further observations on these points are therefore desirable.

For assistance and courtesies extended in connection with these dissections and observations, acknowledgments are due Dr. F. Kebler, pathologist, and Dr. George B. Twitchell, house-physician to the Cincinnati Hospital; also to Messrs. S. Newlin and J. G. Williams, students at Miami College.

To summarize these observations I would conclude:

1. The arachnoid membrane is a true shut sac, similar in structure and function to the serous membranes of the other great cavities. Its parietal layer is easily separable from the dura at the vertex in the fœtus and young infant, but practically inseparable in this region in the adult. At the base of the skull it is demonstrable as a separate membrane even in the adult. To assert that the parietal layer of arachnoid is absent, because its subepithelial connective tissue has fused at the vertex with the dura (connective tissue), is as incorrect as to describe the great omentum as one layer of peritoneum, because its original four layers have become matted and adherent.

2. The arachnoid cavity communicates freely with the subarachnoid space, by means of two foramina situated in the visceral arachnoid, one on either side of the medulla. For these I would propose the name "lunulate foramina," from their crescentic or lunulated edges, produced by the attachments of fibrous bands which cross the openings transversely. Subsequent observations, in two instances, confirm the presence of the "lunulate foramina." In one of these, the basilar process of the occipital and the sphenoid body were cut away from the base and the dura removed, so as to show the foramina *in situ*; thus excluding the possibility of their artificial production during the extraction of the brain.

CINCINNATI, December 16, 1890.

## CONTRIBUTIONS TO THE MORPHOLOGY OF THE BRAIN OF BONY FISHES.

C. L. AND C. JUDSON HERRICK.

### I. — SILURIDÆ. — With Plate XVII.

C. JUDSON HERRICK.

The family Siluridæ, comprising the cat fishes and bull-pouts, forms a very convenient starting point for a discussion of the brain of the teleosts. It is a very close family, at least as far as our inland fresh-water forms are concerned, and at the same time it is distributed in great abundance over the entire North American Continent with considerable diversity of habitat.

Of all the Teleostei the Siluridæ, according to Prof. Cope,<sup>(1)</sup> are more closely related in internal structure to the gars and other ganoids. The brain, however, is as distinctly teleostean as that of any other fish examined and shows very little evidence of any close relationship with the ganoid fishes. On the other hand, the elongation of the olfactory crura, the structure of the cerebrum, the extrusion of the cerebellum and the form of the medulla all suggest affinities with the more highly specialized teleosts, while the brain of some of the other bony fishes, particularly the mud-eating fishes, *Hyodon*, *Dorosoma*, etc., has a very pronounced reptilian aspect. Judging from brain characters alone, the

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<sup>1</sup> Fide Jordan and Gilbert, "Manual," p. 95.



Siluridæ should be placed among the most highly specialized bony fishes, though this, of course, does not necessarily involve a position high in the scale, phylogenetically considered.

The present contribution is based upon the study of dissections and histological preparations of such species of Siluridæ as are most accessible in the Ohio Valley., viz., *Amiurus catus* gill, *Pilodictis olivaris* Gill and Jordan, *Ictalurus punctatus* Jordan, and *Ictalurus lacustris* Gill and Jordon. The adult brains of these species are so nearly alike that it would be difficult to distinguish them externally, and in the following descriptions the statements apply to all of them unless otherwise expressly indicated. In the case of some of our large river cats especially, and probably of the other species also, the brain practically ceases to grow when the fish attains a moderate size, even though the weight of the body may afterward increase many fold. A specimen of the mud cat, *Pilodictis olivaris*, for instance, weighing twenty-one pounds, had a brain which, when hardened, could scarcely be distinguished by careful measurements from that of another specimen weighing less than five pounds. The cranial cavity, however, enlarges more nearly in proportion to the size of the head. In large specimens it is more than twice the size of the brain, which lies in the ventral and caudal portion. In the remaining space an oily arachnoid tissue is closely packed around the emerging nerves. In smaller specimens the brain is much larger in proportion to the head until in individuals one inch long it fills the entire cranial cavity and, in fact, almost the entire head.

*Measurements.*—The following measurement are taken from an alcoholic brain of *Pilodictis olivaris*. Other measurements in the text refer to the same specimen. This fish was 40 cm. long, and would weigh about four pounds. The measurements, however, would be almost equally exact for the brain of a specimen weighing twenty pounds: Length of brain from end of cerebrum to exit of dorsal root of vagus, 17 mm.;

length of cerebrum, 6 mm.; width of cerebrum, 7.5 mm.; width of optic lobes, 10 mm.; width of cerebellum, 11.25 mm.; length of cerebellum in the median median line, 8.5 mm.

*Cranial Nerves.*—Compared with the size of the brain, the cranial nerves are enormous, much larger than in any other fish which has come to our notice. This is a function, doubtless, of the enormous size of the head in the cat fishes. The olfactory nerves are very short, passing directly from the olfactory lobes into the nasal cavities in numerous separate bundles. The optic nerves are long, passing out, in large fish, for several centimetres parallel to the olfactory crura, then diverging at an acute angle to the orbits. They arise from the ventral surface of the thalamus, immediately cephalad of the hypoaria, are quite distinct from each other at the origin and remain so throughout, crossing, however, below the cerebrum. They are not, at first, cylindrical, but very strongly flattened dorso-ventrally. The other cranial nerves may be conveniently divided, after Gegenbaur, into two groups, the trigeminus group and the vagus group. In both of these groups the relations are greatly complicated, not only by the large size of some of the nerve roots, but by the presence of plexi. Only the more important of these are noted, and in the peripheral distribution many of the smaller branches are omitted.

In the trigeminus group the fifth is of supreme importance, and absorbs many of the others. The third arises as a single strand under the caudo-lateral angle of the hypoaria, passes into the fifth and loses its identity completely (Plate XVII, Fig. 4, III). The fourth is minute. It arises from the caudal end of the optic lobe and also passes out with the fifth. The fifth is larger than all of the other cranial nerves combined, and passes out of the cranial cavity by no less than four distinct foramina. These are indicated in approximately their relative positions in Plate XVII, Fig. 5. For convenience of description the various branches of the fifth will be

numbered as in the figure last referred to and treated successively. The branch  $V_1$  is discrete from the others and passes farther dorsad to a separate foramen,  $F_1$ , having previously divided, giving off a large branch ventrad which passes through the foramen  $F_2$ . Before this division it receives a small ramus from  $V_6$ , another from  $V_7$ , and gives one to the combined trunk of  $V_5$  and VII. The dorsal branch of  $V_1$  gives off a small twig before entering its foramen which passes dorsad, then cephalad between the frontal bones. After passing through the foramen it takes its course not far from the median line superficially, giving off various fibres to the frontal region, to terminate in the premaxillary. The more ventral division of  $V_1$ , after passing through the lower foramen,  $F_2$ , is wrapped up with the fibres of  $V_3$  without, however, losing its separate identity, receives at least two separate small strands from  $V_2$ , and passes through the lower part of the orbit, giving off several branches to the infra-orbital region and the region behind and above the angle of the mouth. The branch  $V_2$  is also nearly discrete to its origin. After passing through the foramen  $F_3$ , it gives off the two branches above referred to, several small twigs to the frontal region, two large branches to the posterior nasal barbel, and terminates in several branches in the premaxillary not far from the terminus of the dorsal part of  $V_1$ . It also gives off a considerable branch which supplies the supra-orbital region and passes on to the anterior nasal region. The branch  $V_3$  is nearly distinct from the two preceding, but more closely united with  $V_4$  until after they leave their foramen. It gives off a considerable ramus soon after leaving the foramen, which sinks down to the roof of the mouth and terminates in the dental cavity of the premaxillary. The major part of this branch passes farther laterad through the orbit, giving two large rami to the barble at the angle of the mouth and others to the regions adjacent. Another branch which passes through the foramen  $F_2$  is  $V_4$ , which connects by means of a small ramus with  $V_5$ . After leaving the fora-

men it divides into two. A smaller branch turning caudo-laterad passes to the masseter. The remainder passes through the orbit to the angle of the mouth and infra-maxillary region. The remaining fibres, which pass through the foramen  $F_2$ , are those of  $V_5$  and VII, which are inseparably united for several centimetres. This trunk receives, in addition to the fibres from  $V_1$  and  $V_4$ , referred to above, a small fascicle from  $V_6$ . After leaving the foramen a considerable branch is given off from the cephalic division which dips down and passes caudo-laterad to the depressor operculi. The branches  $V_5$  and VII subsequently partially reunite before their final separation. This plexus may serve the function of a chorda tympani. The more cephalic branch,  $V_5$ , is considered to be the homologue of the inferior maxillary nerve. It gives off a few small fibres to the ental surface of the masseter and then divides. The more superficial division passes cephalad to the infra-maxillary region. The deeper division passes through a foramen in the articulare inferius suspensorii maxillæ (of Meckel) and again divides into a dentary branch penetrating the end of the inferior maxillary into its dental cavity and a mylo-hyoid branch which passes by the end of the inferior maxillary, then cephalad on the ventro-mesal surface of the latter to the inferior barbels, two branches being given to each barbel. Ramus VII, which is considered to be the homologue of the facial nerve, after separating from  $V_5$ , passes laterad, giving off a twig to the levator operculi. Passing then to the ventral surface, it supplies the muscles of that region, apparently those concerned chiefly with deglutition. The carotid plexus, if present, is probably all intra-foraminal. With reference to the first four divisions of the fifth, homologies cannot be pushed very far; and yet it seems legitimate to consider that the more dorsal division of  $V_1$  and  $V_2$  are, roughly speaking, homologous with the orbito-nasal (of Parker), the rest of  $V_1$ ,  $V_3$ , and  $V_4$  with the superior maxillary. Two important divisions of the fifth remain to be considered. The small branch  $V_6$

springs from the base of  $V_7$  very near its origin and passes cephalo-dorsad through a separate foramen,  $F_{11}$ , thence laterad to the opercle, superficially. Before entering its foramen it sends a very small twig cephalad to ramify in the frontal bone near the median line.  $V_7$  is one of the largest separate branches of the fifth nerve. Its apparent origin is not from the medulla, but from the roots of the other divisions. It passes dorso-caudad through a foramen,  $F_4$ , situated over the caudal end of the medulla, thence caudad superficially near the median line the entire length of the body. It appears to partake of the function of the nerve of the lateral line. Gasser's ganglion is obviously developed on this branch alone. The microscope, however, shows elongated bands of ganglion cells between the strands of the other branches also. The sixth nerve could not be separately distinguished. The auditory nerve springs from the medulla immediately caudad of the trigeminal by several roots which are united into a broad, flat band. The cephalic and caudal portions supply the semi-circular canals, the middle portion the otolithic sac.

In the vagus group the ninth and tenth nerves are quite distinct. The ninth arises immediately caudad of the eighth and closely associated with it. After sending a branch to communicate with the ventral root of the vagus it divides, one branch going to the opercle, the other to the first gill. One or two small branches arise near the medulla and pass caudad. Their connections were not discovered. The tenth arises by two large roots, dorsal and ventral, which combine into a ganglion outside the foramen. Cephalad, there branch off from this ganglion nerves to the several gills, one branch to the first and second, another to the second and third, and another to the third and fourth. Each gill thus receives two distinct nerves. Passing caudad, there is a large branch which divides, one portion supplying the levator of the pectoral fin, the other the depressor of the pectoral fin. From the latter arises a small cutaneous branch to the post-



opercular region. Arising from the ganglion of the vagus immediately dorsad of the last is a very small fibre passing to the lower pharyngeal region. Farther dorsad is the visceral branch of the vagus. This gives a small branch to the middle of the fourth gill and a larger one to the organs of the thorax. The main trunk passes caudad and spreads out over the stomach, mesentary, etc. The largest division of the vagus nerve is the nerve of the lateral line. It communicates by a delicate plexus with the nerves of the muscles of the pectoral fin and the cutaneous nerve connected with them, then passes caudad superficially along the lateral line for the whole length of the body. The spinal accessory nerve cannot be separately distinguished. The first spinal nerve, which might, perhaps, with equal propriety be called the twelfth cranial nerve, arises behind the medulla by two roots, dorsal and ventral. The latter is considerably farther cephalad than the former. The two roots remain distinct until after they pass through their foramen (Plate XVII, Fig. 5, *n. s.p.*).

*Rhinencephalon.*—The olfactory lobes in the adult are in immediate proximity to the nasal cavities, and therefore far distant from the rest of the brain. In large specimens the olfactory crura would thus be more than fifteen centimetres long, while the olfactory nerves would be only a few millimetres. In very young specimens one inch long the brain is so large that it fills the whole front part of the head, and the olfactory lobes are in their usual position, closely appressed to the cerebrum. Compare Plate XVII, Fig. 2, with Fig. 3. Each lobe is sub-spherical, three millimetres in diameter, attached to the crus on the caudal aspect, with the fibres of the olfactory nerve springing from the opposite side. The internal structure is very much as in reptilia. Ectad there is a glomerular zone which is well developed, though not so much as in Hyodon. Within this are specific olfactory cells irregularly and sparsely distributed in a single series. They are fusiform to flask-shaped, with the apices usually directed peripherally. The centre of the lobe contains small

dense cells resembling Deiter's cells. There is an olfactory ventricle which extends from the cerebral ventricle the whole length of the crus and well out into the lobe, though not to its centre. It lies in the dorsal part of the lobe and retreats farther dorsad as the lobe passes into the crus. In the crus itself all of the fibres lie ventrad of the ventricle which is bounded laterally, as well as dorsally, merely by a membrane. The entire cavity is lined with epithelium. This membrane is continuous caudad with the pallium of the cerebrum and, with the epithelium of the ventricle, is the apparent homologue, using Prof. Wilder's terminology, of the pes, while the fibrous portion of the crus and the body of the lobe constitute the pero of the olfactory. In the olfactory crus the fibres are gathered into numerous bundles which are separated by layers of small spherical cells. The crus, upon entering the cerebrum, divides into a well-defined radix mesalis and radix lateralis.

*Prosencephalon.*—The mantle portion of the cerebrum is represented, as usual among fishes, only by a delicate transparent membrane, the pallium, lined with epithelium. This pallium is entirely free from the basal portion of the cerebrum on the dorsal and lateral aspects, and below it is free as far mesad as the lateral edge of the radix lateralis of the olfactory, *i.e.*, the sinus rhinalis. The median fissure is not prominent, being represented dorsally by a slight fold of the pallium in the median line. Caudad the pallium is plicated in this region to form a considerable choroid plexus. Cephalad the median fissure is deepened until at the exit of the olfactory crura a similar fold is thrust up from below and the two crura are entirely separated. The pallium, however, continues to envelop the crura, maintaining about the same relations as in the cerebrum, *i.e.*, attached only ventrally, free at the sides and above. Thus the lateral ventricles are continued cephalad into the rhinencephalon, as described above. For a discussion of the cerebral ventricles see beyond.

The basal portion of the cerebrum consists of two lobes which are considered to be the homologues of the axial lobes of the Sauropsida. They are connected below by a membrane which may be considered as a continuation of the pallium, and are otherwise quite distinct from each other except in the region of the anterior commissure. Each lobe is oblong, about as high as it is wide, and about one-fourth longer than it is wide and is attached to the diencephalon by its caudo-ventral angle. The dorsal (ventricular) surface of these lobes is marked with an intricate system of fissures and convolutions, which, however, seem not to be very constant, even in the same species. There are four fissures which are almost always obvious externally, though somewhat variable in size and position. They are found in other fishes quite generally and are here named in accordance with the nomenclature of Prof. C. L. Herrick as given elsewhere in this number. The most strongly-marked and constant fissure is the rhinalic fissure, or sinus rhinalis, on the ventral surface. This marks the line of union between the pallium and the basal lobe. This line passes from the lateral edge of the olfactory crus at its point of exit caudo-laterad to about the centre of the hemisphere; it then turns at an obtuse angle, passing caudo-mesad to the lateral edge of the optic nerve at its exit. The two rhinalic fissures thus define a broad pentagonal depression in which lies the decussation of the optic nerves, and dorsad of which, in the substance of the basal lobes, lie the olfactory crura, and farther caudad, the fibres of the crura cerebri. It is present in other teleostean brains, though not usually as strongly marked as in the Siluridæ, and may be called the rhinalic aspect. On the dorsal surface the most prominent fissure is the frontal fissure, which arises on the fronto-median aspect of the cerebrum from about the middle of the olfactory crus at its exit and passes caudo-laterad in an irregular line almost to the diagonally opposite angle of the basal lobe. Here it meets the occipital fissure, which arises on the latero-caudal aspect

and passes caudo-mesad. By these two fissures there are defined a large mesaxial lobe mesad of the frontal fissure and a narrow occipital lobe caudad of the occipital fissure. The fourth important fissure is the Sylvian, which is not so strongly developed as the preceding. It arises on the ventral surface in the centre of the lateral aspect and passes dorsad. This fissure, with the occipital, defines a triangular lobe, with the apex directed ventrad, the cuneate lobe. Behind the cuneate and ventrad of the occipital lobe, from which it is separated by a small fissure, is a large lobe which may be called the temporal lobe, though in the cat fish it occupies the caudo-ventral end of the cerebrum. The term hippocampal lobe is applied to the lip, or ventral extrusion, just laterad of the sinus rhinalis. Cephalad there is another small fissure which may be considered as a part of the rhinalis. It arises from the lateral edge of the radix lateralis, passes dorsad and, with the frontal fissure, circumscribes a frontal lobe. This lobe lies immediately dorsad of the olfactory crus and is very small. There is still another noteworthy fissure in the median sinus between the two basal lobes. It runs in each lobe longitudinally in both directions from the anterior commissure. It is best observed in transection. There are other small fissures on the dorsal surface, but they seem not to be constant and are considered unimportant. It is to be remembered that all of these fissures, except the rhinalis and possibly the Sylvian, are spurious fissures and are not to be homologized with the cerebral fissures of higher animals. That is, they are fissures of the axial lobe, not of the cortex, for this dorsal surface is a ventricular surface and is clothed with epithelium, like the pallium. The epithelium here, however, tends to be more columnar than that of the pallium.

To understand the full significance of these lobes it will be necessary to examine the cellular histology of the cerebrum in some detail. A transection cephalad to the anterior commissure reveals three areas sharply differentiated histo-

logically. The mesaxial lobe is characterized by small flask-cells, with large granular nuclei and dense nucleoli. They are very closely packed, with a strong tendency toward a zonary arrangement. The lateral lobe is characterized by similar elements more sparingly distributed, but still showing an evident zonary arrangement. This latter is particularly true ventrally. Dorsally the cells are less numerous, and those of the type found in the central lobe predominate. The central lobe lies between the two last mentioned and typically does not appear on the dorsal surface, being triangular with the apex directed dorsad. The cat fishes, however, present a marked exception to the latter point. The histological elements are large cells lying in a clear stroma. They are spindle-shaped or multiangular, all with very large processes, large circular nuclei and dense nucleoli. The central lobe is nowhere sharply separated from the lateral lobe. On the other hand, the frontal fissure separates it very clearly from the mesaxial lobe, especially peripherally. The structure of the occipital lobe closely resembles that of the central, while the temporal lobe has the small cells of the mesaxial, somewhat less abundant, but with the same zonary arrangement.

The prosencephalon, as a whole, is considerably larger than the optic lobes, but very much smaller than the cerebellum. It attains to about the average size as compared with other Teleostei thus far examined.

*Diencephalon.*—The thalamus in the adult cat fish is entirely hidden from the dorsal aspect by the optic lobes and the cerebellum. Even the attachment of the epiphysis is obscured by the forward extension of the cerebellum. The epiphysis is very much as in some Lacertilia. It arises as a small membranous tube lined with epithelium immediately cephalad of the superior commissure, passes dorsad enwrapped by the plexus which fills this region, then turns abruptly cephalad passing under the cerebellum and over the cerebrum. It lies in the shallow median fissure in intimate



contact with the pallium as far cephalad as the exit of the olfactory crura, then turns dorsad to the roof of the cranial cavity. The diameter of the tube is about .1 mm. at the base, but increases slightly as it passes out. About the base of the epiphysis the membranous roof of the third ventricle is inflated dorsad to form a small closed sac which is nearly spherical and about 1 mm. in diameter. This represents the dorsal sac, which is so conspicuous a feature in many fish brains. In this case it is entirely obscured from view in the brain before dissection by the over-arching cerebellum. The walls of this sac are intricately plicated, the folds embracing the base of the epiphysis and forming what has been previously mentioned as the homologue of the choroid plexus. The epiphysis is related to the roof of the cerebral ventricles cephalad in essentially the same way; *i.e.*, it is imbedded in the pallium and surrounded by it. Thus morphologically the dorsal sac is produced forward nearly to the end of the cerebrum, though its cavity has been all but obliterated.

On the ventral aspect the hypoaria and hypophysis cover nearly the entire cephalic portion of the brain. Each hypoarium is a pear-shaped body, flattened dorso-ventrally, with the smaller end directed cephalad and the more concave surface mesad. At the cephalic end of each hypoarium is a small tubercle lying immediately ventrad to the lateral portion of the optic nerve at its exit from the brain. In the adult the hypoaria are divaricated cephalad by the cinereum. This body is cordate with the apex directed caudad, and is somewhat over half as long as the hypoaria. Attached to its apex and lying in the narrow cleft between the caudal ends of the hypoaria is the saccus vasculosus, which, in large brains, sometimes attains a diameter of 3 mm. This is a membranous sac, the base of which, lying between the hypoaria, is filled with a vascular plexus, resembling in structure the vascular portion of the epiphysis of higher animals. The more expanded portion, overlying the larger ends of the hypoaria, is discoid or sub-spherical, more delicate

in texture and dilated with fluid. Immediately caudad of the saccus vasculosus a large blood-vessel enters the brain in the median line. This is always present and seems to represent the area perforata posterior of higher brains. The broader end of the cinereum is directed cephalad and is indented in the median line by a deep sinus extending to its centre. This point is the most ventral projection of the cinereum, and from it the infundibulum passes out into the hypophysis. This appendage is slightly ovoid, with the larger end directed cephalad, 4.5 mm. long by 3.5 mm. wide and high. The stipe is filiform, slightly thicker at the base and attached to the body of the hypophysis at a point about one-fourth of the distance from the caudal end of the latter. The hypophysis is solid, and of a uniform texture.

*Mesencephalon.*—The portion of each optic lobe which is exposed is ovoid, with the larger end directed cephalad and the long axis passing obliquely dorso-caudad. The two lobes are widely divaricated by the cerebellum. The roof of the mesencephalon is depressed, thin, and devoid of cellular elements, except internally in the tori longitudinales (“fornix” of authors) adjacent to the ventricle. The mesencephalon does not reach the ventral surface of the brain at any point. In this region, cephalad, that surface is entirely occupied by the hypoaria, while the portion caudad of the hypoaria is to be considered a forward extension of the medulla, as in higher animals.

*Ependecephalon.*—In this group of fishes the cerebellum is the most characteristic feature. It consists of two major divisions, one external and one internal. Both are well developed, the former to an unusual degree. The whole mass of the first division is folded upon itself at an angle of  $90^{\circ}$ , thrust cephalad, and closely appressed to the subjacent optic lobes and hemispheres. The entire extent of the fourth ventricle is thus exposed, in striking contrast to the brains of most other fishes. As viewed from above, the cerebellum is nearly rectangular, with a lateral expansion caudad, and it

extends forward far enough to cover a quarter of the cerebrum. This portion is oval in transection with the longer axis horizontal. Caudad, at the point of union with the médulla, it expands to a width greater than that of the brain at any other point. The two lateral lobes thus produced contain white matter, chiefly in the form of fibres, passing caudad into the medulla, and are to be considered as portions of that body, homologous in part with the restiform bodies. They lie farther caudad than the cerebellum proper, one on each side of the fourth ventricle over about the middle of the medulla. A small transverse fissure is present on the dorsal surface of the cerebellum, a few millimetres cephalad of the fourth ventricle. Between this fissure and the fourth ventricle are transverse fibres passing apparently from one lateral lobe to that on the opposite side. Cephalad of this fissure the grey and white matter are arranged in the usual manner, the grey filling the centre and enveloped by the white. White fibres enter the cerebellum from below in the centre of the grey matter and thus form a sort of arbor vitæ, as in higher animals. In the median line, about 1 mm. cephalad of the to the caudal end of the cerebellum, a very narrow ventricle arises from the aqueduct of Sylvius and passes dorsad into the cerebellum for about two-thirds of the way to its dorsal surface. With this exception the cerebellum is solid.

The internal division, or *volvula*, lies in the aqueduct of Sylvius immediately cephalad of the small ventricle of the cerebellum. It presents the appearance of having been formed by folding back upon itself through an angle of  $90^{\circ}$ , not the entire cerebellum, as before, but merely the half which lies cephalad to the cerebellar ventricle. It is as if that half had projected much farther ventrad than the other half, as a free lip, and had then been bent cephalad into a horizontal position. Thus the grey matter which normally lies next the cerebellar ventricle becomes ventral adjacent to the aqueduct of Sylvius, and the white matter becomes dorsal adjacent to the roof of the optic lobes. This *volvula* is about

half as long as the exposed part of the cerebellum, and is thrust cephalad into the third ventricle nearly to the superior commissure.

*Metencephalon.*—The medulla is remarkable for its great depth, as well as its great width. The width is due, in large measure, to the presence of the wide, lateral lobes connected with the descending tracts of the cerebellum. The depth is, in part, due to the great development of the two pairs of dorsal tuberosities. Of these the cephalic or trigeminal tubers are much the larger. They rise in the floor of the fourth ventricle to a height nearly as great as that of the cerebellum. They are strictly intra-ventricular, and are covered by the membranous roof of the ventricle. The interior is occupied by fibres and cells pertaining chiefly to the trigeminal nerves. The other pair of prominences, the vagal tubers, are, for the most part, extra-ventricular. The fourth ventricle lies between them, and its membranous roof extends from the mesal surface of the one to that of the other. Most of the fibres of the dorsal root of the vagus take their origin from this pair of tuberosities. Behind the vagal tuberosities the fourth ventricle closes. Its caudal limit is marked by an elevated ridge, or crest, of transverse fibres. Farther caudad, at the exit of the so called first spinal nerve, the medulla is thickened on both dorsal and ventral surfaces, behind which it passes at once into the spinal cord. On the ventral surface there is another considerable thickening at the exit of the trigeminus. The ventral surface otherwise presents very few features of note. The ventral fissure, too, is not so deep as the dorsal. The cranial nerves are discussed elsewhere in this article.

*Ventricles.*—In discussing the encephalic ventricles we shall pass from the spinal cord cephalad. The canalis spinalis is very small. It gradually enlarges in the medulla up to the exit of the dorsal root of the vagus, where it is suddenly extended dorsad to the surface, thus forming the fourth ventricle. From this point the ventricle is very deep, but

quite narrow until the vagal tubers are passed, after which it rapidly expands until at the exit of the ventral root of the vagus it occupies the whole dorsal surface, not excepting the lateral lobes or cerebellar peduncles. Farther forward the ventricle contracts into the aqueduct of Sylvius and passes under the cerebellum, into which it sends a very narrow arm. This cerebellar ventricle passes directly dorsad and does not turn cephalad with the cerebellum. Immediately cephalad of the *volvula* the aqueduct expands into the third ventricle, which, at the same time, communicates laterally, by wide openings, with the ventricles of the optic lobes near their cephalic ends. The latter bodies are hollow throughout their entire length, though the ventricle is much larger cephalad. In this region the triangular ventral part of the third ventricle is bridged over by the superior commissure, and from this point forward severs its connection with the dorsal part. The *torus longitudinalis* (*fornix*) very soon comes into contact with the superior commissure, and thus separates the ventricles of the two optic lobes again near their cephalic ends. Beneath the superior commissure the third ventricle dips suddenly ventrad in the form of a narrow cleft, reaching to the surface. In its descent it sends two branches laterad into the *hypoaria*, expands in the *cinereum*, and then sends an arm caudad into the *saccus vasculosus* and another cephalad into the *infundibulum*. The ventricle of the *cinereum* lies in about the centre of that body. It is about one-third as wide as the *cinereum*, but very thin dorso-ventrally. Ventrad of this expansion the third ventricle gives off a very small branch on each side (.5 mm. in diameter) which is lined with very strong epithelium and extends caudad near the median line between the *hypoaria* for some distance into the base of the *saccus vasculosus*. The ventricles of the *hypoaria* are crescent-shaped, diminishing caudad to sub-triangular and oval. Just cephalad of the superior commissure the *epiphysis* arises from the dorsal surface, as above described. Cephalad of the dorsal sac the third ventricle passes into the cerebral



ventricles by a wide foramen of Monro. Aula and portæ can scarcely be separately distinguished. The median fissure is so poorly developed that the lateral ventricles of the two hemispheres are practically continuous for the whole length of the cerebrum. The limits of the cerebral ventricles are implied in the description of the pallium given above. They pass from the median fissure laterad to the sinus rhinalis of each side and envelop the entire cephalic aspect of the basal lobes. The basal lobes are entirely separated, except in the region of the anterior commissure, by the cerebral ventricle, down, even to the extreme ventral limit of the cerebrum, where the ventricle is bounded by a membranous floor. The relations of the cerebral ventricles to the ventricles of the olfactory lobes are discussed in the section devoted to the rhinencephalon.

#### DESCRIPTION OF PLATE XVII.

*Fig. 1.* Dorsal view of the brain of the adult mud cat fish, or yellow cat, *Pilodictis olivaris* Gill and Jordon. The olfactory lobes, with most of the crura, have been removed. The trigeminal, vagus and first spinal nerve-roots are shown.  $\times 2$ .

*Fig. 2.* Dorsal view of the brain of a young bull-pout, *Amiurus catus* Gill, three inches long. The olfactory lobes have been removed.  $\times 4$ .

*Fig. 3.* Dorsal view of the brain of a much younger bull-pout, one inch long. The olfactory crura are reduced until the olfactory lobes are closely appressed to the hemispheres.  $\times 10$ .

*Fig. 4.* Ventral view of the brain of the adult mud cat, *Pilodictis olivaris*. The olfactory lobes, hypophysis and saccus vasculosus have been removed. The Roman numerals refer to cranial nerves.  $\times 2$ .

*Fig. 5.* Lateral view of the brain of *Pilodictis olivaris*, designed to illustrate the distribution of the cranial nerves. The various nerve-roots are retained, as nearly as may be, in their natural positions. The olfactory lobes have been removed; *ol.*, olfactory crus; *u. op.*, optic nerve;  $V_1, V_2, V_3, V_4, V_5, V_6, V_7$ , the seven principal branches of the trigeminus nerve;  $F_1, F_2, F_3, F_4$ , the four principal foramina of the trigeminus nerve; *VII*, the facial nerve; *u. dep. op.*, nerve of the depressor operculi; *u. lev. op.*, nerve of the levator operculi; *VIII*, acoustic nerve; *IX*, glosso-pharyngeal nerve; *gX*, ganglion of the vagus nerve; *u. ll.*, nerve of the lateral line; *X visc.*, visceral branch of the vagus; *X th.*, thoracic branch of the vagus; *u. d. p.*, nerve of the depressor of the pectoral fin; *u. l. p.*, nerve of the levator of the pectoral

fin; *I*, *II*, *III*, *IV*., nerves to the four gills, respectively; *n. sp.*, the first spinal nerves.

For full discussion of these nerves see text under *cranial nerves*.

*Fig. 6.* Transection of cerebrum of *Ictalurus* cephalad of the anterior commissure.

*Fig. 7.* Transection of the same brain at the level of the præ-commissura, *Prec.* The tracts from the olfactory radices are seen in section dorsad of the præcommissura on either side the median line. *O. tr.*, optic tracts; *Ped.*, peduncular fibres.

*Fig. 8.* Transection of the same brain at the level of the habena, *H.*; *Cer.*, cerebellum.

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## II.—STUDIES ON THE BRAINS OF SOME AMERICAN FRESH-WATER FISHES.

C. L. HERRICK.

### A.—TOPOGRAPHY.

The olfactory lobes have an essentially similar structure throughout the various families of Teleosts, but there is a great variation in position, which is a function of the position of the nasal capsules and the form of the cranial cavity.

Every gradation between an olfactory lobe closely soldered to the cerebrum and one separated by many times the length of the whole brain from the hemispheres may be encountered in our fresh-water fishes. The gizzard-shad (*Dorosoma*), which has a decidedly reptilian brain, is an illustration of the first type (Figs. 6-7, Plate XIX). Sections of the olfactories of this species in front of the cerebrum are semi-oval, with the larger extremity of the oval dorsad. A shallow groove occupies the middle of the dorsal surface. In section, the membranes may tend to separate from the lobe, but there is no true ventricle. At this level the lobe is composed of the usual glomerular structure with Deiter's nuclei, and the whole is richly supplied with small vessels.

The glomerules are chiefly massed ectad. The nervous elements are small and inconspicuous.

The cerebrum overlaps the olfactory dorsally, and the lateral ventricle descends to the level of the olfactory mesally, but is separated from the crus by a small spur of the cerebrum. Gradually the olfactory lobe narrows into the crus, and is embraced by the cerebrum laterad as well as mesad. The cerebrum is completely enveloped by the palium and ventricle except near the attachment of the crus and thence some distance laterad to beyond the rhinalis fissure or sinus of the ventral surface. There is a dense collection of fusiform cells mesad of the crus on either side of the ventricle. The latter represents a forward protrusion of the third ventricle rather than the aula. The centre of the crus is occupied by a tract, while others gather about the rhinalis sinus. The first mentioned tract can be easily traced as far caudad as to the anterior (or interlobular) commissure, where it turns mesad, decussates with its fellow and continues in nearly the same relative position toward the thalamus upon the opposite side. Other fibres derived from the crus follow the rhinalis sinus and constitute a distinct radix lateralis which can be traced to a point opposite to the commissure, where they seem to enter the hippocampal lobe, to be described beyond, although part may pass directly mesad to the commissure.

In *Hyodon* (the moon-eye) the olfactory lobes are unusually large and lie some distance from the cerebrum, while the lateral ventricles extend well out upon the dorsal surface of the crura cephalad of the cerebrum. The crura are accordingly flattened, and enter the meso-cephalic angle of the cerebral lobes in two partially distinct radices. The radix lateralis is smaller, and spreads out about the sinus rhinalis in the form of a series of small bundles. The radix mesalis is a large bundle, which retains its position in the ventromesal angle of the cerebrum as far caudad as the anterior commissure.

The buffalo fish (*Carpiodes*) furnishes an illustration of long-stalked olfactories. The crura are enormously elongate and the ventricles extend a long distance upon the dorsal surface of the crura proper, being covered by a thin pallium similar to that of the hemispheres.

The arrangement is well seen in Fig. 1, Plate XIX, where the dorsal pallium has been removed from the cerebrum but remains on the crura. The sections (Figs. 4-5, Plate XXI) illustrate substantially the same arrangement as seen in the black-horse (*Cycleptus*). The radix lateralis is wider than its fellow and very thin vertically, while the radix mesalis is rather compact and enters the ventro-mesal angle of the cerebral hemispheres.

The radix lateralis first becomes attached to the cerebrum by its lateral border. Then the mesal radix becomes attached to the mesaxial lobe, which is here quite distinct, thus cutting off a spur of the ventricle, which remains distinct some distance caudad. The connection with the common ventricle or aula is upon the cephalic aspect, affording evidence that the portæ in this case may almost be said to lie entirely cephalad of the hemispheres. The forward extension of the ventricles beyond the cerebrum is, we believe, a fact of primary importance in understanding the morphological significance of fish brains. The subsequent course of the two radices are distinct, and corresponds to that described in the black-horse (*Cycleptus*), which furnishes one of the best illustrations of the tubular olfactory crus. Transverse sections show that the arrangement of ventricles, etc., is the same as that described by my brother in the cat-fish. The transection of the crus cephalad of the cerebrum shows it to be composed of a tubular sheath of membrane, with the fibres collected in two somewhat distinct bundles along the ventral surface, entering the radix lateralis and mesalis respectively. There is, however, a narrow band of fibres between the sheath and the epithelium lining the ventricle. The ventricle passes into that of the cerebrum at a point where the

latter entirely surrounds the frontal projection of the hemispheres. The pallium thus embraces both the olfactory and cerebrum before the olfactory enters the hemisphere (see Plate XX, Figs. 1-4).

In Siluroid fishes the olfactory lobes are stalked in the adult. The two radices are scarcely distinct before entrance into the cerebrum, but at once separate thereafter. According to C. Judson Herrick, the ventricles enwrap the crura nearly completely throughout their course (see above for details.)

In the eel the olfactory lobes are relatively large and sessile (Plate XIX, Figs. 9-11), and are overlapped by the hemispheres, which are lunulate in section. The mesaxial lobe is distinct but large, and receives the radix mesalis on the ventro-mesal angle. The two radices appear before the crus enters the hemisphere.

In the eel, more easily than in any other fish examined, the course of the radix mesalis can be clearly traced. The tract preserves its identity fully, and crosses as an entirely distinct bundle of the hippocampal element of the anterior commissure. After decussating it reappears in the corresponding position on the opposite side, and can be traced to the medi-dorsal part of the thalamus. The radix lateralis follows cephalad to the region of the anterior commissure, where it turns suddenly mesad and crosses through the peduncular bundles and unites with the tract of the radix mesalis and decussates with the latter. The fibres of both of these radices are light-colored, while the bulk of the anterior commissure fibres are very dark. Horizontal sections especially leave no doubt as to the course pursued by these fibres, though, of course, the possibility is not excluded that other connections exist, especially with the cell masses corresponding to the hippocampus.

In the buffalo fish (*Carpiodes*) longitudinal sections seem to show that part, at least, of the fibres of the radix lateralis pass to the hippocampal lobe.



## SUMMARY OF OLFACTORY LOBES.

1. The olfactory lobes are exceedingly variable in size and position, but exhibit no decided differences in structure.

2. The primary condition is similar to the permanent condition in Sauropsida, *i.e.*, the lobes are sessile or attached by short crura to the base of the cerebrum; but their connection with the cerebrum is more accidental than essential.

3. Whether they become stalked or not depends on whether the growth of the head removes the peripheral organs of smell from the brain at an early period, and whether, in case it is so removed, the olfactory nerve or crus is elongated. The probable determinant for the latter is the relative rate of development of the various regions of the head. The olfactories are always sessile in an early stage.

4. The crura contain two distinct tracts, forming a radix mesalis and lateralis.

5. The lateral ventricle is frequently extended into the the crura, but the form it assumes varies. In the extreme case the crus is a hollow cylinder, with the fibres chiefly collected in the ventral portion. In other cases the ventricle simply extends a short distance along the dorsal surface of the crus.

6. In some cases there is a rudimentary olfactory ventricle in the substance of the lobe.

7. The radix mesalis enters a special mesaxial lobe of the cerebrum and its fibres decussate in the commissura interloborum, forming with the next a hippocampal commissure and fornix.

8. The radix lateralis follows a gentle groove (sinus rhinalis) on the ventral surface of the hemispheres to a point opposite the decussation of the radix mesalis when it turns abruptly mesad and crosses to the opposite side; but probably also gives off fibres to the hippocampus. According to Owen the olfactory lobes are sessile in *Perca*, *Scomber*, *Esox*, *Pleuronectes*, *Blennius*, *Anguilla*, *Gasterosteus*, *Eper-*

lanus, Cottus, Trigla, Amblyopsis, Echeneis, the Ganoidei and Lepidosiren; and long-stalked in Salmo, Cyprinus, Brama, Tinca, Gadus, Lota, Hippoglossus, Clupea, Belone, Leucoperca, Cobitis, Plectognathi and Plagiostomi.

*The Cerebrum.*—The topography of the cerebrum cannot be satisfactorily discussed until much extended and careful observations have been accumulated. In the groups examined it is relatively constant, and such differences as appear are often less important than they at first seem. The form varies chiefly as a result of the varying size and position of adjacent portions of the brain. The dorsal view usually presents a sub-quadrangular outline, tending to oval. From the side one may observe a rudimentary fissure and curvature corresponding to the fissure of Sylvius of higher brains. The transverse section is nearly always sub-triangular, with the curved base of the triangle dorsad. The cerebrum presents three well-marked aspects: a mesal surface, facing the median fissure (in cases where the pallium of the two hemispheres fuses completely this aspect is absent or represented solely by the corresponding aspect of the axial lobe); a dorso-lateral aspect, generally one continuous curved surface; and, third, a ventral or rhinalic aspect. The last mentioned surface differs from the others in being chiefly a non-cortical or axial surface, as is the case in the corresponding area of higher brains. It is bounded laterally by a more or less distinct fissure or sinus, the rhinalis sinus, which is more distinct, cephalad. This fissure is the undoubted homologue of the rhinalis fissure of higher vertebrates in so much as the radix lateralis of the olfactory crus occupies the adjacent region. The pallium separates at this point. It must be constantly kept in mind that the fissures upon the dorsal surface of the cerebrum of fishes cannot have the same significance as the cortical fissures of mammals. The Sylvian fissure, however, seems to be obscurely indicated by a depression near the middle of the lateral surface, which results from an incipient flexure. There are upon the dorsal surface a number of de-

pressions, which are impressed upon the axial lobe, and may or may not be obvious before the removal of the pallium. Three of these are especially constant. First, *the frontal fissure*, separating the *mesaxial lobe* superficially from the remainder of the cerebrum. This fissure begins upon the cephalic or ventral surface and extends parallel to the longitudinal fissure a longer or shorter distance upon the dorsal surface. The *occipital fissure* occupies an analogous position upon the occipital region, and in extreme cases unites with the frontal to form an occipito-frontal groove. The third fissure is the dorsal portion of the *Sylvian fissure*, and extends a variable distance toward the occipito-frontal.

By the aid of these external landmarks and the variations in internal structure, a few pretty well-marked regions of the axial lobe may be conveniently designated. The *mesaxial lobe* is that region bordering the longitudinal fissure and limited laterally by the frontal fissure. The *central lobe* is an ill-defined region, with few large spindle cells lying in the central and ventral portions of the cerebrum. In some cases there is a well-defined line of demarkation between this and adjoining areas. It is in the ventral portion of this lobe that the peduncles enter the cerebrum, and it may be looked upon as forming in a special sense the homologue of the striatum. The *lateral* or *parietal lobe* embraces the lateral portions of the cerebrum, and, though frequently imperfectly defined externally, differs in cellular structure sufficiently to make its recognition possible. A small lobule lying between the Sylvian and occipital fissures may be called the *cuneus* without implying any homologies with higher brains (see Fig. 1, Plate XIX). An *occipital lobe* may be recognized in the caudad projection lying adjacent to the habenæ, and a *temporal lobe* upon the caudo-lateral aspects behind the Sylvian fissure. There is a caudo-ventral projection which is invariably present, and, from its being the starting-point of the posterior part of the pallium, may be compared to a hippocampus, and will be referred to as the hippocampal lobule.

*The Thalamus.*—In general, it may be admitted that Baer correctly characterized this region in the statement, “Es sieht so aus, als ob das Mittelhirn das Zwischenhirn unterdrückt habe.” The strong optic nerves and tracts serve to constrict the organ greatly and obscure the original form. In some cases the origin of the epiphysis and habena are visible from above, while in others, like the black-horse, the mesencephalon is thrust forward by the great development of the volvula, so as to cover much of the cerebrum itself. Apparently, as a result of the constriction of the middle of the thalamus, it is forced caudad, and, to supply the requisite nervous material, develops the hypoaria or inferior lobes, which, instead of representing the mammillary bodies, seem to contain the homologues of the displaced walls of the median part of the thalamus. The saccus vasculosus marks the caudad extension of the thalamus. It seems necessary to recognize three parts of the thalamus, as follows. *The præthalamus:* This includes the ventral median region caudad of the anterior commissure and ventrad of the hippocampal lobules. It is quite distinct from the adjacent parts of the cerebrum, and contains the various tracts passing from it toward the lower parts of the brain. *The mid-thalamus* is that part which corresponds to the principal part of the organ in reptiles and bears the habena. Its caudal limit may be recognized in the inferior commissure. Caudad of the this, and extending as far as the saccus vasculosus, is a portion which is covered dorsad by the optic lobes, and bears laterally the hypoaria. This may be termed the *post-thalamus*.

There is no difficulty in recognizing these divisions in any of the Teleosts examined.

*Mesencephalon.*—The topography of the optic lobes differs from that of reptiles only by reason of the greater or less invasion of the optic ventricle by the volvula. Transections of the mesencephalon of the eel cephalad resemble corresponding sections of the turtle closely. There is a slight pro-

jection into the ventricle from the base, forming the colliculus or torus, with the concentric arrangement of cells characteristic of the colliculi, and the rather thick tectum exhibits the same pronounced stratification of elements. Along the median dorsal line the dependent ridges known as the tori longitudinalis are evident, though relatively small, and seem to make up for the slight development of the granular zone of the tectum.

In the drum the extensive development of the volvula, and its compact plication within the ventricle serve to greatly modify the tectum and other bodies. The whole organ is tilted forward so that the apparent cephalic aspect really represents a large part of the dorsal. The tori are therefore cut longitudinally in transections cephalad, so that their apparent size is increased. On the dorsal surface, however, the tectum is forced apart, and the tori form the starting points for the membranous expansion which bridges over the interval separating the two halves. The colliculi are likewise thrust apart and modified as to form by the same means.

The black-horse affords an illustration of an extreme modification resulting from the exceptional development of the volvula. The mesencephalon in this case extends far cephalad over the hemispheres, while its entire dorsal surface is reduced to a membrane. The tori are thus extended in the same plane as the tectum, and serve as supports for the membranous roofs (Plate XIX, Fig. 4). The position and structure of the corpus posterior will be discussed in the histological part of this paper, as will the cranial nerves.

*The Cerebellum.*—The present notes may be regarded as supplementary to the earlier paper on the architectonic of the cerebellum. In it we attempted to show that the variations in structure exhibited in different groups could all be reduced to a common type and their differences explained by tracing the invaginations and evaginations of the walls of the fourth ventricle. No better illustration of this principle



could be selected than that furnished by the Teleosts. The cerebellum is the most variable, and, at the same time, the most characteristic segment of the brain. It varies greatly even in the same group, yet the plan of structure is constant and is even suited to characterize families and genera. The structural peculiarity which is characteristic of all fishes is the volvula (valvula of authors). This organ may be briefly defined as a modification of that part of the roof of the aqueduct of Sylvius which lies between the valve and the tectum. Its structure is essentially that of the cerebellum, and it is directly connected with the tectum cephalad. The extent to which it develops seems to depend upon a variety of circumstances. When for any reason the cerebellum fails to acquire the normal size the volvula may compensate therefor. The size of the cerebellum as a whole (including volvula) is undoubtedly a function of the activity of the fish. Thus, for example, the black-horse and buffalo-fish are allied systematically and live in the same streams, but the former is a very active carp, while the latter is sluggish and massive. The main portion of the cerebellum is of relatively the same size in the two fishes, but a glance at Plate XIX, Figs. 1 and 4, will convince one that the development of the volvula in the black-horse corresponds to its active habits. In the typical cases the volvula is but a forward fold into the optic ventricle, but numerous secondary modifications obscure this primitive simplicity. It may be well to refer to several illustrations at this point, remembering that the cerebellum is mechanically the least stable of the structures of the brain. The axial portion of the organ is a thickening of the roof of the fourth ventricle. The caudal and lateral aspects of the roof are reduced to a membranous velum or infolded to form a plexus, while the cephalic boundary is altered to form the velum anterior or volvula. Thus the only rigid attachment of the cerebellum is that formed from the relatively small pedunculi. Rotations in all directions except cephalad meet with no opposition, and the absence of closed cranial walls permits

the resulting organ to occupy almost any portion with reference to the axis of the brain.

The moon-eye, *Hyodon*, is perhaps the most reptilian brain of the osseous fishes here noticed, and has the simplest cerebellum. It is probably one of the best types in which to study the architectonic of the cerebellum and optic lobes in comparison with those of reptiles. The optic lobes are large and almost absolutely unmodified by the cerebellum, except in so far as the corpora posteriores are thrust ventrad and laterad. The volvula is well developed, and its dorsal lamina passes directly into the tectum. The valve is small. Immediately caudad of the valve the cerebellum swells into a large, thick sac which soon becomes free from the walls of the medulla. The cavity of the cerebellar ventricle is not suppressed, and there is very little to suggest the complicated projections of the calamus and vagus regions of the medulla found in most fishes, especially the carps. The cerebellum thus forms a simple lobe, projecting over the partly exposed opening of the fourth ventricle. It is relatively small, as may be gathered by a comparison with corresponding views of the Gizzard-shad (Plate XIX, Fig. 7).

As in *Lepidosteus*, the cephalic part of the mesencephalic ventricle is not entered by the volvula. Transections in front of the oculomotor roots resemble similar sections of reptilian brains, except for the presence of the small hypoaria. The *tori longitudinalis*, or appendages of the median line of the tectum, are large.

The volvula extends cephalad to just in front of the third nerve-roots where it appears two-lobed, having the apparently ectal (ventricular) surface composed of gray matter, a median zone of Purkinje's cells, and a central mass of white matter. Farther caudad the cavity due to the invagination is encountered, surrounded by the white zone, which is, therefore, morphologically ectal. The dorsal wall of the sac thins out and passes into the membranous caudal wall of the optic lobes, which are obviously paired at this level.

The fourth nerves pass caudad to the optic lobes, around which they arch, and enter the narrow, slit-like opening of the volvula and then continue cephalad nearly to the level of the caudal margin of the hypoaria, where they meet and dip suddenly ventrad into the substance of the valve, then, after decussating, they continue cephalad to the ventrolateral margin of the valve, and, arching about the aqueduct, enter the nidulus near the median line and adjacent to the aqueduct and bounded ventrad by the dorso-median fasciculus.

Caudad of the valve the roof of the fourth ventricle expands and thickens into the median lobe or vermiforme of the cerebellum, being for sometime connected with the lateral walls of the ventricle by thick lateral lobes which have not the structure of the cerebellum, but contain an intimate mixture of granules, nerve-cells and fibres. The cerebellum proper is, as above said, simply a caudad pouch from the roof of the fourth ventricle, which, however, remains for some distance in contact with a mass similar in composition to the lateral lobes which forms the transition into the velum posterior, and is homologous with the "bursa" of the sturgeons.

In the gizzard-shad, although the brain is so similar to the moon-eye, externally, the cerebellum is remarkably modified in details of structure. What at first gives great trouble, is the fact that in the axial part of the cerebellum or vermiform lobe the gray matter is apparently ectad instead of internal.

To a point about one-third the length of the optic lobes from their caudal boundary the relations are as above. The volvula is small, and its cavity nearly closed. The cerebellum proper is driven forward between the optic lobes, and especially dorsad, so that, as though by actual lateral pressure, the organ is thrust together upon itself and its dorsal and cephalic surfaces are folded in along the median line and the lateral white matter is reduced to a mere membrane, only recognized by careful examination. The appearance of lateral compression in the fungiform contours

is remarkably verified in transverse section. A caudad diverticle of the cul-de-sac from the exterior extends to the level of the valve where the fourth nerve enters without the curvature described in the moon-eye, but which is here unnecessary by reason of the divarication of the optic lobes. At this level the cerebellum is obviously folded upon a longitudinal fissure for almost its whole height, though the fissure has been practically obliterated by the union of the walls. A little caudad a rudiment of the caudal diverticle of the fourth ventricle can be detected, and the arrangement of the gray and white matter shows that the duplication has been affected in the usual manner, yet the cavity is absent, and the whole organ is so closely adherent to the combined lateral lobes that only a comparison with simpler types explains the seeming anomalies.

This case is very instructive as showing how far the distortion and secondary union of parts may obscure perfectly simple homologies.

In the eel the cerebellum may be characterized as a simple depressed variety with small volvula. In striking contrast to the gizzard shad, the modifications are such as could most easily be referred to the effects of pressure from above. The volvula is exceptionally small. The fourth nerve enters directly behind the optic lobes, decussating in a very obvious and uncomplicated valve. The dorsal lamina of the volvula passes into the tectum opticum with but a short velum cerebelli anterior. Caudad of the trochlearis there is a slight pocket and corresponding revolution cephalad. Then for some distance the cerebellum is a simple thickened dorsal wall of the fourth ventricle which, nevertheless, has the appearance of having been thrust ventrally into that cavity, with the result of thrusting the ventricular gray layer of the cerebellum laterad and dorsad, so that it is thicker on the lateral than the ventral aspects and projects on either side as a slight protuberance on the lateral margin of the dorsal surface. The caudad portion of the cerebellum is a sac-like

diverticle, the lumen of which has been extinguished by the same ventrad pressure, so that the dorsal and ventral granular layers adhere and fuse in the centre. Some evidence of the cavity still remains, however, in spurious lateral recesses, consisting only of membrane connecting the partially everted lateral portions of this ventricular layer. The posterior portion of the cerebellum is thus reduced to a double leaf-like valve over the calamus region.

In Cyprinoid fishes the cerebellum is greatly developed, but strictly the same principle is followed as indicated above. The volvula is highly developed and complicated. The connection between the dorsal lamina of the volvula and the caudo-lateral edges of the optic tectum is affected well cephalad near the median line between the tori longitudinalis. Behind the valve there is a sudden dorsal expansion containing a moderate cephalad protrusion of the cerebellar ventricle, which latter is connected by a dorsally elongated strait with the fourth ventricle. The posterior part of the cerebellum is free and directed obliquely dorso-caudad, and is flattened somewhat. The caudad protrusion of the ventricle thus becomes a mere line or is indicated only by the fused granular zones of the dorsal and ventral lamina. The lateral lobes of the cerebellum are very large.

In the buffalo-fish, *Carpiodes*, the cerebellum has a strong but not exaggerated development. The optic lobes, in consequence, are thrust cephalad and moderately dilated. The volvula is enormously developed and thrust forward. Its most remarkable peculiarity is that cephalad it becomes bifurcate. The dorsal lamina is fused with the ventral for much of its length, and the granular portion of the dorsal lamina is present only near the tip. The lamina becomes free caudad and unites with the velum near the median line, as in the carp, though the union does not take place so far within the optic lobes and the tori extend far out on the velum.

In the region of the valve the lower lamina is greatly thickened. Except that the cephalad diverticle of the cere-



bellar ventricle is somewhat larger; the remainder of the cerebellum is precisely as in the carp.

In the older individuals the great lateral expansion of the volvula is remarkable.

The extreme in this type of cerebellar differentiation is reached in the black horse, *Cycleptus elongatus*. In this case the optic lobes are thrust far cephalad over the cerebrum and expanded laterally like a hood. The tectum is wedged apart and the two tori are connected by a wide stretch of thin membrane only. The volvula is enormous, and consists of a central and two lateral lobes, in which the simple fold, which is the real source of the structure, is effectually obscured. The lateral lobes are pushed cephalad as divergen tuberosities. The appearance is as though these bodies had been formed by excessive lateral growth, which, among other things, had removed the granular layer entirely from the dorsal lamina and then crumpled the whole organ by lateral pressure. The middle lobe is morphologically the ventral lamina, which is thrust between the the two moities of the dorsal lamina.

This explanation solves the apparently unreconcilable conditions. The lateral lobes or severed portions of the dorsal lamina of the volvula extend far caudad of the point where the ventral lamina emerges as the roof of the fourth ventricle or vermiform portion of the cerebellum.

The presence of these two latero-caudal excrescences on either side of the median portion of the cerebellum is the obvious external cause of a median infolding of its dorsal roof, which is indicated even in the external view by the groove seen in Fig. 4, Plate XIX. In transverse sections the fold is seen to be an exceedingly deep one, though the edges coalesce completely.

The remainder of the cerebellum is as in the carp, except that the mode of connection with the medulla is modified by the lateral pockets containing the divaricated caudal protrusions of the volvula.

The cat-fish group presents more remarkable variations, which have been explained in detail by C. Judson Herrick.

In the drum the most remarkable peculiarity of the mid-region of the brain is its relative shortness; the cerebellum is crowded far dorsad and lies perched, as it were, between the trigeminal lobes and the vertically elongate optic lobes. The great dorsal elevation and corresponding shortening of the optic lobes could not fail to exert a greatly modifying influence on the volvula, which in these fishes is very large. The result is seen in a curious multiple folding of the dorsal lamina in the frontal plane; so that successive lobes appear in transverse section. The remainder of the cerebellum shows no other effect of the compression than that exhibited in its position and a slight cephalo-dorsal protuberance.

The examples cited are sufficient to show that the most divergent types may easily be reduced to a single fundamental form.

The *cranial nerves* have not been carefully studied in this connection, because of an exigency of publication, nor has there been opportunity to compare the papers of Prof. Wright on the cranial nerves of the cat fish. In the cat fish the exaggerated development of the trigeminal system is well illustrated in the earlier installment of this series, by C. Judson Herrick.

In the drum (*Haploidonotus*) the following relations prevail: The vagus consists of two nearly equal branches, one of which springs from the caudal portion of the vagal tuberosity, while the other is derived from the extreme cephalic portion, and both are apparently derived from nearly the same dorso-ventral level. The two branches remain distinct for some distance, so that the cephalad root has an independent course, nearly twice as long as that of its fellow. At their union a more or less distinct ganglion is developed. From the latter the small nerve of the lateral line arises. A visceral branch and a branch probably supplying the pectoral fin-muscles follow, and then five branches to the gills, the

caudal one dividing peripherally. The ninth nerve is much smaller than either branch of the vagus, and arises from the caudo-ventral aspect of the very tumid trigeminal lobe, a short distance caudad of the eighth. It soon receives a small anastomosing branch from the cephalic root of the vagus, which returns to the latter a little farther peripherad, but proximad of the ganglion. The distribution of the ninth is as described in the cat fish.

The eighth has two distinct roots, but the cephalic branch is closely associated with the seventh, which is distinct from the fifth beyond Gasser's ganglion, and is distributed to the opercular and gular regions.

At its roots the fifth nerve is composed of three chief divisions, but beyond the ganglion there are five, the most dorsal of which is the trigeminal accessory nerve of the lateral line.

The sixth is small, and no separate root was found. The third and fourth are small, but normal, and the remaining nerves offer no peculiarities.

#### PLATE XIX.

*Fig. 1.* Dorsal view of the brain of the buffalo-fish, *Carpiodes tumidus*, B. and G. *L.v g.*, vagal lobes; VIII, eighth nerve; *Ma. l.*, mesaxial lobe of the cerebrum; *Cun. l.*, cuneate lobe; *L. l.*, lateral lobe; *Op.*, optic nerve.

*Fig. 2.* Lateral view of the same brain. *Hyp.*, hypophysis; *F. oc.*, occipital fissure; *F. Syl.*, Sylvian fissure; *V l d.*, dorsal root of cephalic division of trigeminus; *V l v.*, ventral division of the same; *V l.*, caudal trigeminus.

*Figs. 3-5.* Three views of the brain of the black-horse, *Cycleptus elongatus*. *Hyp.*, hypophysis; *T. cin.*, tuber cinereum; *vg. l.*, vagal lobe; *Hpa.*, hypoaria.

*Figs. 6-7.* Lateral and dorsal views of the brain of the gizzard-shad, *Dorosoma cepedianum*.

*Fig. 8.* Dorsal view of the brain of the moon-eye, *Hyodon tergisus*. The hemispheres are divaricated and deprived of the pallium.

*Figs. 9-11.* Three views of the brain of the common eel.

#### PLATE XX.

A series of transections of the brain of the black-horse, *Cycleptus elongatus*. A description of histological details will be given in a subsequent paper.

*Fig. 1.* Section at the union of the olfactoria with the rhinalic aspect of the hemispheres. *Op. n.*, optic nerve.

*Fig. 2.* Section somewhat caudad of the above. *Lat. l.*, lateral lobe; *Mesa. l.*, mesaxial lobe; *F. rhin.*, rhinalis fissure.

*Fig. 3.* Section cephalad of the decussation of the optic nerves. The cerebrum is here overarched by the mesencephalon and the volvula. *Hip. l.*, hippocampal lobe; *volv.*, volvula cerebelli.

*Fig. 4.* Section at the decussation of the optic nerves. *Torus long.*, torus longitudinalis; *Membr. tect.*, the tela tecti or membranous portion of the tectum opticum.

*Fig. 5.* Section through the præthalamus, *pre. th.*

*Fig. 6.* Section through the mid-thalamus. *H.*, habena.

*Fig. 7.* Section cephalad to hypoaria. *M. b.*, Meynert's bundle.

*Fig. 8.* Section through post-thalamus.

*Fig. 9.* Section at the caudal level of the hypoaria. Region of mesencephalic decussations. *Aq. S.*, aqueduct of Sylvius.

*Fig. 10.* Section at the beginning of the cerebellum.

*Figs. 11-13.* Successive sections through the medulla and cerebellum. Description will be deferred to subsequent installment.

#### PLATE XXI.

*Figs. 1-3.* Sections through the medulla of the black-horse, continuing the series of Plate XX. *Lb. trigem.*, trigeminal lobe; *L. vagi*, vagal lobes or tubers. Details will be given in later installment.

*Figs. 4-5.* Transections through the olfactory crura and cerebrum. *Fig. 4* is some distance cephalad of *Fig. 5*, and on the opposite (left) side.

*Figs. 7-10.* Transections of the brain of *Dorosoma*.

*Fig. 7.* Section at the anterior commissure.

*Fig. 8.* Section at the superior commissure.

*Fig. 9.* Section at the exit of the third nerve.

*Fig. 10.* Section at the caudal level of the optic lobes to illustrate the great induplication of the cerebellum along the median (line at a). The suppressed lateral ventricle, or recessus lateralis, with its membranous lateral walls is indicated at *ventr. lat. cerebel.*

## THE DEVELOPMENT OF THE CRANIAL NERVES OF VERTEBRATES.<sup>(1)</sup>

PROFESSOR C. VON KUPFFER.

*Gentlemen:*

There is scarcely need of the assurance that I do not stand before you with the pretense of presenting the comprehensive subject of my report with perfect symmetry on all sides. That would only be possible if the development of the vertebrate head as a whole could receive thorough treatment at the same time. The works which relate to the cranial nerves are still issuing, and it is difficult to predict, up to the present, how the course of these works will influence the solution of the problem of the vertebrate head.

In consideration of the time here allotted to such a report, I limit my remarks to a condensed summary of the present trend and results of research in relation solely to the *morphogeny* of the cranial nerves, apart from their histogeny and from the remaining phases of the problem of the head.

So much may be said in advance: that in the formation of the vertebrate head very remarkable reductions and fusions of endodermal and mesodermal parts, and, in connection therewith, of the peripheral nervous system, extending in direction from before backwards, have occurred. And, further, I venture to assert that, besides a branchial system

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<sup>1</sup> Report read at the meeting of the Anatomical Society at its fifth annual session, at Munich, May 18, 1891. Translated for this journal, from advance sheets, by OLIVER S. STRONG, Fellow in Biology in Columbia University.



of cranial nerves, sharply distinguishable genetically from the spinal system and belonging to the gill apparatus, a spinal system of dorsal nerves has likewise more or less completely maintained itself.

The old theory of the spinal nature of the cranial nerves, dating its beginnings from Proschaska and Sömmering, received weighty support through the Goethe-Oken vertebrate theory of the skull; it outlasted the latter doctrine, and appeared until recently consistent with Bell's law. But the embryological works of the last decade have so severely shaken the foundations of this doctrine that so decided a defender of it as C. Gegenbaur<sup>(1)</sup> found himself obliged to admit that the homodynamy of the cranial and spinal nerves appeared to him no longer tenable. The first shock this theory received was through the observation of Balfour,<sup>(2)</sup> on elasmobranch embryos, that the mixed cranial nerves are decidedly of dorsal origin, and they are also to be distinguished essentially from the dorsal roots of spinal nerves owing to the motor elements in them.

While Balfour did not succeed in finding in the region of the cranial nerves any roots whatever which might be compared with the ventral roots of the spinal nerves, he, on the other hand, did not doubt the complete validity of Bell's law, and accordingly advanced the hypothesis that there had existed originally a common fundamental form of the nerves in the whole body which are only represented by the dorsal roots of a mixed nature. At this stage the differentiation of head and trunk took place, so that the type of the spinal nerves corresponding to Bell's law would be regarded as secondarily acquired, while the cranial nerves have preserved the original condition. This hypothesis appeared to Balfour so much the more probable in that he

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<sup>1</sup> "The Metamerism of the Head and the Vertebrate Theory of the Cranial Skeleton," *Morph. Jahrb.*, XIII, p. 64 and 104.

<sup>2</sup> "The Development of the Elasmobranch Fishes," *Journal Anat. and Phys.*, Vol. XI, 1877, and *Handbook of Comp. Anat.*, trans. by Vetter, Jena, 1887, Bd. II, p. 411.

decided,<sup>(1)</sup> in opposition to the observations of Stieda<sup>(2)</sup> and Schneider,<sup>(3)</sup> that in *Amphioxus* ventral motor roots were lacking.

This hypothesis appeared untenable, since, on the one hand, ventral spinal nerves of a motor nature are found in *Amphioxus*, and, on the other hand, the development of ventral nerves was observed in the region of the head, as, for example, the origin of the abducens from the ventral aspect of the medulla in the chick, as well as in *Scyllium*, by Marshall.

But, aside from the hypothesis, the fact remains that the undoubtedly dorsal cranial nerves do not conform to Bell's law, but are of a mixed nature.

Van Wihje's<sup>(4)</sup> treatise, appearing soon after the works of Balfour above mentioned, brought to light the new disclosures, known to you, concerning the ontogeny of the cranial nerves in Selachians as proof, on one side, that at least two pairs of muscle nerves in the head, the oculomotor and abducens, appear after the manner of the ventral spinal nerve roots, and, like these, innervate only muscles arising, as alleged, from somites, to which the eye-muscles should belong; while the motor elements of the cranial nerves arising dorsally are confined to the innervation of the muscles of the visceral arches, which proceed from the lateral plates. Relying upon this observation, Van Wihje impeached the validity of Bell's law, and showed the possibility that the relations discovered for the head have further application in the trunk, as in the enunciation of Bell's law the vegetative muscles in the trunk proceeding from the lateral plates were left out of consideration.

While Van Wihje sought in this way to establish the

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1 "On the Spinal Nerves of *Amphioxus*," *Quart. Jour. Mic. Soc.*, Jan., 1880, p. 90.

2 "Studies on *Amphioxus Lanceolatus*," *Mem. d. l'Academ. d. Sc. de St. Petersburg*, 1873, I. 46.

3 "Contrib. to the Comp. Anat. and Devel. of Vert.," Berlin, 1878, p. 15.

4 "On the Mesodermsegments and the Development of the Nerves of the Selachian Head," Amsterdam, 1882.

agreement between cranial and spinal nerves, he himself discovered at the same time facts which cause the distinction between both groups to appear more marked than was hitherto supposed. On one side, he shows that the dorsal cranial nerves in respect to their course bear relations to the somites entirely different from the spinal nerves, and it furthermore emerges from his investigations that the epidermis participates in the development of the peripheral twigs of the cranial nerves, as Götte<sup>(1)</sup> and Semper<sup>(2)</sup> had already affirmed for the N. lateralis vagi.

Concerning the relation to the mesoderm, the dorsal cranial nerves first take their course over the mesoderm and on between the somites and the epidermis, but the dorsal roots of spinal nerves pass within and below the somites. This distinction is so important that it was especially by this that C. Gegenbaur was driven to abandon the homodynamy of cranial and spinal nerves, which he had previously defended.

According to Van Wihje's discovery, the facial, glosso-pharyngeus and vagus enter into close connection with the epidermis in a double row of points. On the one hand, fusion of their ventral branches occurs at the upper hinder side of the gill cleft which lies cephalad; on the other hand, the rudiments (Anlage) of their dorsal branches fuse with thickened portions of the epidermis. From the dorsal places of connection are developed portions of the lateral-line system with its nerves, in such a way that Van Wihje thought the participation of elements of the epidermis in the formation of the nerves might be regarded as certain. From the places of fusion of the ventral branches with the epithelium of the gill clefts the terminal twigs of those branches are developed.

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1 "Embryology of the Toad."

2 "Uro-genital System of Plagiostomes," *Arbeiten aus d. Zool.-Zoot. Institute zu Würzburg*, Bd. II, p. 398.

A. Froriep<sup>(1)</sup> has pointed out the part played by the epidermis in the development of the cranial nerves in mammalian embryos, where, in comparison with the condition discovered by Van Wihje in Elasmobranchs, the share of the epidermis in this process seems scarcely less important. In cow embryos such processes take place in the region of the facial, glosso-pharyngeal and vagus, whose course is briefly as follows: In embryos 8-9 mm. long with three gill furrows apparent outside and four pharyngeal pouches, the spindle-shaped ganglion of the facial unites with a pit-like, sunken and at the same time greatly thickened place in the epidermis, which corresponds to the dorsal extremity of the first external gill furrow. The same thing occurs with the glosso-pharyngeus; here also the distal end of the ganglion in the rudiment of this nerve unites with a greatly thickened and depressed portion of the epidermis dorsad to the second pharyngeal cleft. The vagus rudiment behaves similarly. Its large ganglion locates itself adjacent to a thickened epidermal surface, of the shape of a figure 8, which is situated dorsad to the third gill furrow and the vicinity of the fourth.

In cow embryos 15 mm. long the connections of the facial and glosso-pharyngeus are lost, but not of the vagus, and here the thickened mass of epidermis reaches deep into the ganglion, so that the two components cannot be definitely separated from each other.

Froriep compares these "organs of the gill clefts," though with reserve, to the connections, described by Van Wihje, of the ventral branches of the same nerves with the epidermis, dorsally to the gill clefts, and explains them as rudiments of sense organs which do not attain further development, and probably belong in the category of organs of the lateral line but with which they cannot be fully homologous, since the lateral organs of fishes are formed on the dorsal branches of the cranial nerves. As those ganglia which enter

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<sup>1</sup> "Rudiments of Sense-organs in the Facial, Glosso-pharyngeal and Vagus," Arch. f. Anat. u. Physiol., Anat. Abth., 1885.

into the connections under discussion and accordingly originate through a union of central with epidermoid elements, Frioriep indicates the gang. geniculi, gang. petrosum and gang. nodosum; they exhibit the phylogenetic remnants of former sense organs; they cannot consequently be considered homologous with the spinal ganglia, and thereby fails a chief support of the spinal hypothesis. The nerves of the visceral arches as segmental nerves can no longer be identified with spinal nerves.

In a long series of works J. Beard<sup>(1)</sup> has handled the problem of the cranial nerves and their sensory end organs. *Torpedo ocellata* furnished the principal object of Beard's investigations, although sharks, teleosts, Amphibia and Amniota (*Lacerta*, chick) came under consideration. In the main, Beard follows, in facts as well as in the interpretation of the conditions, the observations and conceptions of the previously mentioned investigators, but also contributes the fact that the participation of the epidermis in the formation of ganglia and nerves occurs also in the region of the trigeminus.

The complete representation of the development of a dorsal cranial nerve would, according to him, be as follows: The rudiments of the ganglia in the head, agreeing throughout with those of the spinal nerves, arise as differentiations of the inner layer of the ectoderm, just outside the limits of the neural plate. They separate from the ectoderm, become displaced upwards in the closing of the neural tube, and come to lie between its lips, but are always distinguishable from it. After the closure of the neural tube, the portion of

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1 "On the Segmental Sense Organs of the Lateral Line and on the Morphology of the Vertebrate Auditory Organ," *Zool. Anz.*, 1884, p. 123; "The System of Branchial Sense Organs and their Associated Ganglia in Ichthyopsida," *Quart. Jour. Microsc. Sc.*, 1886, Vol. XXVI, new series, p. 95; "The Ciliary or Motor-Oculi Gangl. and the Gangl. of the Ophthal. Profund. in Sharks," *Anat. Anz.*, 1887, p. 585; "The Old Mouth and the New," *Anat. Anz.*, 1888, p. 15; "A Contribution to the Morphology and Development of the Nervous Syst. of Verteb.," *Anat. Anz.*, 1888, pp. 874, 899; "The Development of the Peripheral Nerv. Syst. of Vertebr.," *Quart. Jour. Microsc. Sc.*, Vol. XXIX, new series, 1889, p. 153; "Prof. Rabl on the Mode of Development of the Vertebrate Peripheral Nervous System," *Anat. Anz.*, 1890, p. 125.



these rudiments corresponding to each cranial nerve grows ventrad, unites with the central organ by means of root fibres, probably growing out centripetally, and comes to lie on the *outer side* of the mesoderm, between this and the epidermis; while the rudiments of the spinal ganglia (of the trunk) proceed ventrally on the inner side of the mesoderm, thus between this and the central organ. These cranial ganglia rudiments, designated by Beard "*neuralganglia*," fuse at the level of the chorda with a thickened place in the epidermis dorsad of the neighboring gill cleft, which thickening represents externally the rudiment of a "branchial sense organ," internally that of a ganglion belonging to the latter, the "*lateral ganglion*." Here the elements of the neural and lateral ganglia blend indistinguishably with each other; there thus arises the definitive and apparently single ganglion of the cranial nerve in question. This separates from the epidermis—that is, from the rudiment of the branchial sense organ—but remains connected with the latter by a nerve strand, the *suprabranchial nerve* (dorsal branch of Van Wihje). From the ganglion are developed distally three nerves, namely, the *N. præbranchialis*, *N. postbranchialis*, and *N. pharyngeus*. As to the *N. suprabranchialis*, it is, according to Beard, clear that it arises from the epidermis; for the *N. præbranchialis* he accepts the same mode of formation. With regard to the two other nerves, he remains undecided whether the epidermis takes part in their formation.<sup>(1)</sup> Beard regards it as certain in the case of the postbranchial twigs of the *vagus*<sup>(2)</sup> and in the case of the trigeminus (*mandibularis*).<sup>(3)</sup>

For the trigeminus the same law of formation is said to obtain, inasmuch as the mouth represents a pair of gill clefts. But where gill clefts, with the musculature belonging, have entirely disappeared, yet sense organs persist, there, according to this author, the structure is simplified; the *N. post-* and

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1 Quart. Jour. Mic. Sc., Vol. XXVI, 1886, p. 102.

2 Ibidem, p. 110.

3 Ibidem, p. 113

præbranchialis disappear, and the sole ones remaining are the N. suprbranchiales.

As such may be regarded: (1) The N. olfactorius (I segment), more clearly so after it was shown, through the olfactory buds discovered by Blaue, that the organ of smell belongs to the system of the lateral line, *i.e.*, the branchial sense organs. 2. The ophthalmicus profundus (II segment), whose meso-cephalic ganglion (Gn. ciliare, Van Wihje, His) fuses with the epidermis close above and behind the eyes; later this root unites with that of the trigeminus, and the Gn. meso-cephalicum with the Gn. Gasseri.<sup>(1)</sup> 3. The acusticus (VI segment), which is regarded as a remnant of a segmental nerve. The development of the nerve, of its ganglion, and of the ear, corresponds essentially to that of the homodynamous parts of complete segments. The auditory vesicle is the persistent, functionally modified branchial sense organ; the pertaining segment remains in the hyoid arch. Whether the aborted gill cleft is to be found, as Van Wihje thinks; behind the facial, or, as Dohrn takes it, is to be sought before the hyoid cleft, remains undecided.

Regarding the relation of cranial to spinal nerves, Beard at first declared himself in complete agreement with Froriep in so far as the dorsal roots and ganglia of the one could not be homologized with those of the other. Possibly Balfour was right, that the cranial nerves showed a more primitive condition than the spinal nerves, but it may be doubtful whether the spinal nerves ever had the same primitive character.<sup>(2)</sup> Later he changes this opinion, and, in regard to the supposed similar method of formation of the first ganglion rudiment in head and trunk, declares that there is a *partial* homology between the neural ganglia of the head and the spinal ganglia, but the first might possibly be only homologous with the sympathetic portions of the latter.<sup>(3)</sup>

1 Anat. Anz., 1887, p. 565.

2 Quart. Jour. Mic. Sc., Vol. XXVI, 1886, p. 142-143.

3 Quart. Jour. Mic. Sc., Vol. XXIX, 1889, p. 253.

Judging from this, the entirely different position of the neural cranial ganglia on the one hand, of the spinal ganglia on the other, relative to the dorsal mesoderm, was not taken into account by Beard in the comparison.

In a recently published article<sup>(1)</sup> on the development of *Petromyzon Planeri*, I have likewise treated of the method of formation of the peripheral nervous system, in the course of which the previous works of Scott and Shipley on the same object received thorough consideration.

On the one hand, my observations not only yielded a confirmation of the participation, discovered in *Gnathostomata*, of the peripheral regions of the epidermis in the development of the cranial nerves, but caused this participation to appear still more considerable than could be admitted from what was previously known. But, on the other hand, facts emerged which do not accord with the results of the above mentioned authors, and display the complicated nature of the cranial nerves in a new light.

I was then led to essentially the following conception of the composition of the dorsal cranial nerves: Each one is composed of two parts, a *spinal* and a *lateral*, which latter, comprising all its components, can also be designated as *branchial*. The first behaves, with respect to its origin, its course and its relation to the dorsal mesoderm, entirely like a dorsal spinal nerve of the trunk. The dorsal cranial nerves thus originally contain parts homodynamous with the spinal nerves, but thereto is added the second variously formed component, which, arising with the spinal, proceeds over the dorsal border of the mesoderm and is situated on the outer side, between mesoderm and epidermis. It is these lateral components of the cranial nerves into whose composition growths of the epidermis enter, and that occurs in two series lying the one above the other. I distinguished them as *lateral* and *epibranchial* ganglia. The first lie in the hori-

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1 "The Development of *Petromyzon Planeri*," Arch. f. Mik. Anat., Bd. 35, 1890.

zontal plane of the auditory vesicle, and arise at three separate places, *i.e.*, in the region of the trigeminus, acustico-facialis and vagus. The epibranchial ganglia likewise emerge discretely, and there is always one close above each gill pouch. The part of the corresponding cranial nerve proceeding over and outside the mesoderm secondarily unites with these structures, and, indeed, the union with the lateral ganglia is of such a nature that the rudiment of the nerve itself swells into a new ganglion, the *medial* (neural ganglion, Beard). From this union of the medial and lateral ganglia proceeds the definitive ganglion (Hauptganglion) of the cranial nerve concerned. The epibranchial ganglia take part in the development of the terminal twigs of the cranial nerves. In the separation of the lateral, as well as the epibranchial ganglia from the epidermis, there is nowhere shown the rudiment of a sense organ. With the sole exception of the auditory vesicle, which is formed in the closest proximity to the lateral ganglion of the acustico-facialis region and is homodynamous with this lateral ganglion, all these ganglia of both series are entirely independent structures, standing in no connection with principal sense organs.

These were the results which I had reached. I had to break off these investigations, on account of lack of material, at a stage in which the formation of the peripheral nervous system is far from concluded. It was the moment of the escape of the larvæ (from the egg). I have since, with new and more complete material, carried the work on further, and extended it to the stage of larvæ 4 mm. in length. At the same time I discovered that my older material, upon which the work cited had been based, contained gaps which prevented me from arriving at a complete understanding of the earliest beginnings of the cranial nerves. After interpolation of the then lacking stages of development, it is necessary to complete in many respects and partially correct my earlier representation.

The first rudiment I have sufficiently described and

drawn. Towards the conclusion of the folding process taking place in the ectoderm, by means of which the massive central organ is formed, but before its separation from the ectoderm, one sees in the fore half of the embryo (head region) three cords, the median neural and the paired lateral cords, which latter, on either side, correspond entirely to the intermediate fascicles (*Zwischenstrang*) of His (Fig. 1 z).<sup>(1)</sup> But I have not ascertained the succeeding phase since, as I now see, I have lacked the connecting links. I assumed that in the separation from the ectoderm the paired—*i.e.*, the intermediate—fascicles came at the same time to lie on both sides of the median neural cord, that is to say, of the massive brain. That is not the case; the paired rudiments move farther mesad together, so that they unite dorsad of the brain cord, into a plate lying between this and the epidermis (Fig. 2 d P), and which is distinguished from the regularly biserially arranged elongated epithelium-like cells of the brain by reason of the irregular and, subsequently, loose disposition of their elements. This plate exhibits the same structure which His had already sketched, in 1879, in a *Scyllium* embryo and Beard more recently has drawn in various elasmobranchs and of the chick.

Not to anticipate the difficult question as to which parts of the peripheral nervous system are derived from this plate, in our terminology I will refer to it neither as ganglion- nor nerve-plate, but call it the *dorsal brain-plate*, since, although divided into three segments, it extends over the whole length of the brain. Furthermore, in the spinal cord I find the plate not so distinct and represented by a double row of cells, which my pupil, Dr. Victor Rohon, has first described,<sup>(2)</sup> albeit from later stages, in the trout.

Next the cells of the dorsal brain-plate advance laterad

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<sup>1</sup> Compare my drawings in the *Arch. f. Mikr. Anat.*, 1890, Bd. 35, Taf. XXVIII, Fig. 25, and His' figure in the *Arch. f. Anat. u. Phys.*, 1879, Anat. Abt., p. 465.

<sup>2</sup> "On the Histiog. of the Spinal Cord of the Trout," *Sitzgsber. d. math. physik. Kl. d. K. Bayer. Acad. d. W., Munchen*, 1884, Heft I, p. 39.



between brain and epidermis, forming the well-known ganglion- or nerve-“border” (Leiste) of writers, and now it becomes necessary in considering the development of the cranial nerves to keep distinctly in mind the different regions.

I distinguish accordingly: (1) The region of the fore head to the eye, inclusive; (2) the fore gill region, comprising the mouth and the three fore gill pouches; (3) the hind gill region to the eighth gill pouch, inclusive; (4) the trunk region.

In the *region of the fore head* (Fig. 3) begins the formation of the borders (Leiste), which I designate as root-borders (Wurzelleiste), from the dorsal brain-plate, before the formation of the eye has begun; and the cells soon extend along the whole lateral surface of the fore-brain, whereby the connection with the brain here becomes severed. These cells are at first rounded, then become spindle-shaped and touch each other, so that they appear in connected layers. They are ranged mostly in two rows, but so that in one place a larger collection always shows itself. In my treatise I gave a figure<sup>(1)</sup> of this, indicated this accumulation as a ganglion, and regarded it as the first rudiment of the first trigeminus ganglion. That it behaves like the rudiment of a ganglion I still hold, but I have come to doubt whether it goes into the first trigeminus ganglion or forms the first spinal ganglion, to be mentioned later. The determination is difficult, and requires more extended and especially more comparative investigations. But the whole mass of cells does not in every case collect itself into a compact ganglion, but it arranges itself in lines, which, after the appearance of the sense organs, extend both towards the nose and eye and also towards the hypophysial pouch. Later they unite, in the main, with the first trigeminus ganglion, whose branches they appear.

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1 Arch. f. Mikrosk. Anat., Bd. 35, 1890. Taf. XXIX, Fig. 39 g).

In the *fore gill region*, which extends from the eye to the third primitive gill pouch, the process takes place otherwise. Here the mesoderm occurs in addition, which, until the time of the appearance of the dorsal root-borders at the brain, still shows an entirely epithelial arrangement. There are nowhere present detached cells which enter into the formation of connective tissue.

The root-border grows on rapidly to the dorsal border of mesoderm, and spreads out so that it lies cap-like upon the border cells of the mesoderm (Fig. 4). Then two tracts (Züge) of cells separate, of which the inner proceeds between mesoderm and brain, while the other grows on laterad from the mesoderm between it and the epidermis. This latter course is characteristic of the fore gill region. It is wanting in the hind gill region and in the trunk.

As these tracts (Züge) display separate rudiments, I choose for them exact designations. I call the inner tract, which remains in connection with the dorsal border of mesoderm and proceeds ventrad between brain and mesoderm, the *dorsal spinal nerve*, since this rudiment extends in the same way in all parts of the body; the outer tract I designate the *branchial nerve* (Figs. 5 and 6, *nb*).

The border (Leiste), and what proceeds from it, is not continuous in the fore gill region, but at the beginning is divided into three successive segments, which correspond to the regions of the trigeminus, acustico-facialis and vagus, and consists exclusively of elongated, serially arranged cells.

While the separation of the border into the tracts mentioned, the spinal and the branchial rudiments, takes place over the dorsal border of mesoderm—it takes place about the time of the appearance of the eye-rudiment—growths of the epidermis begin in three places; they are the trigeminus, the acustico-facialis and the vagus swellings. They lie laterad of the dorsal mesoderm, and arise, not simultaneously but successively, from before backwards. The method of formation of these swellings I have minutely

described and drawn in my article. But I must here, on the basis of later investigations, make some additions and corrections.

The trigeminus swelling, appearing close behind the eye-rudiment, forms a projection (Fig. 4, *gl*) directed entad and dorsad, and consisting of closely crowded cells, upon which, although still continuous, may be noticed two prominences lying the one behind and under the other. The root of the branchial nerve grows toward this swelling, unites with it by means of a tract of cells, and passes along, with another tract close by, growing in a ventral direction. The growth of these nerve-rudiments results partly from division of these cells, partly through the invasion of new elements from the dorsal brain-plate. At the point of junction of the root of the branchial nerve with the swelling of epidermis, there results a multiplication of the cells belonging to the nerve whereby two heaps of cells, corresponding to the two prominences on the swelling, arise, the elements of which are inserted between the epidermis cells of the swelling, so that later on they could not be distinguished according to their origin.

From this complex two ganglia are isolated successively with simultaneous separation from the epidermis, each of which consists of two parts, one epidermal and one arising from the dorsal brain-plate, of which the first part has been designated by me the *lateral*, the other as the *medial* ganglion (Figs. 5 and 7, *gl*, *gm*). But the two parts are gradually merged into each other, so that finally no clear boundary between them can be pointed out. It is thus necessary to designate the whole body as one, and I propose the term "*principal*" ganglion (Hauptganglion) for it. There belong to the trigeminus two *principal* ganglia, formed in the same way, the *first* and the *second*. The two are *homodynamous*. I correct herewith my earlier view that the first trigeminus ganglion is exclusively of central origin, and has the same value as the medial part of the second trigeminus

ganglion.<sup>(1)</sup> A more complete series of stages has subsequently convinced me of the incorrectness of this view.

The first trigeminus ganglion lies before and over the second, can always be distinguished from this and is connected with the nerve-rudiments of the fore head.

The epidermal swelling next behind gives rise to the *labyrinth vesicle* and the lateral part of the *facialis ganglion*, as likewise homodynamous parts, a portion of its cells also entering into the rudiment of the glossopharyngeus. Vesicle and ganglion arise in close connection, so that in the beginning of the invagination of the pit of the labyrinth, the ganglion is situated within, like a large knob, on the wall of the pit. It becomes further enlarged through proliferation of the cells of the wall. The root of the pertaining branchial nerve itself enters by way of addition, as well with the ganglion as with labyrinth vesicle, and stretches to one other part in this structure, lengthening in a ventral part. The ganglion acquires a median portion from the latter.

The third epidermal swelling, which belongs to the *vagus*, is more stimple than the two preceding. There proceeds from it a rounded, simple lateral ganglion, which, however, by means of the root of the pertaining branchial nerve connecting with it, acquires a considerable medial part and thereby becomes a principal ganglion.

During the formation of this principal ganglion, and before it has yet completely separated from the epidermis, there appear new growths of the epidermis. They lead, in like manner, to the formation of ganglia, without the connection with them of rudiments of sense organs, at least directly. These are the *epibranchial ganglia* (Figs. 4, 6, 7 ge). They arise singly, close above the three primitive gill pouches, and lie thus in a second series removed ventrally from that of the principal ganglia. The epibranchial ganglion appearing first is not the formost, but

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1 Arch. f. Mikr. Anat., Bd. 35, 1890, S. 538.

the one over the second gill pouch. At the end of the embryonic period, and after the release of the larvæ, this process advances cephalad into the region of the trigeminus, and also caudad in proportion as the hind gill pouches successively arise. These ganglia thus exhibit regular branchiomerism, and those arising in the region of the trigeminus point to aborted anterior gill pouches.

How the branchial nerves, passing along by the principal ganglia and proceeding to the visceral arches, connect with the epibranchial ganglia, I shall show later.

In the *hind gill region*, from the fourth primary gill pouch to the eighth, the development of the peripheral nervous system shows a less complicated course. The border (*leiste*) growing out from the dorsal brain-plate appears first as a continuous one, connects with the dorsal border cells of the mesoderm segments and sends a ventral extension between brain and mesoderm; there thus arises from it only the dorsal spinal nerve, the rudiment of branchial nerves remains apart from the border. There nevertheless arise, as already mentioned, in regular order from the epidermis, the epibranchial ganglia corresponding to the gill pouches of this region.

So long as the rudiments of the nerves consist of continuous chains of cells, it is not difficult to follow their course and establish the connections. But there comes a stage where, connected with the cells, fibrillæ appear and separate the cells, and with this difficulty ensues for the investigation, so long as the fibrillæ are not united into thicker cords. The latter has occurred after the release of the embryo, so the investigation is prosecuted on a firmer basis. One can then enumerate the roots in the different regions, and follow the ramifications of the distal nerves. The stage intervening between the first rudiment, consisting of continuous rows, and the later first evident compact nerve cords renders uncommonly difficult the determination of the question whether the rudiments and ganglia proceeding



from the dorsal brain-plate and border respectively at any time give up their connection with the dorsal region of the brain. I assume this separation *only* for the *region of the fore-brain*, where the rudiments also possess secondarily no connection with this region of the brain, but are united with the trigeminus and the mid-brain respectively. Behind this it does not occur, at least not up to the point of time when the formations of ganglia from epidermis begin and come forth in connection with the roots of the branchial nerves. With this question is bound up the other question of the final fate of the dorsal brain-plate. Do its cells advance in a body laterad and ventrad, or a middle portion of the cells of the plate remain in loco, while these cells intercalate themselves in the epithelial covering of the neural tube? According to my observations the latter takes place. A great part of the plate is applied to the formation of the peripheral nerves, but the remainder appears wedged in between the cells of the roof of the brain without the interruption of the connection with the peripheral parts.

I do not propose to discuss the histogeny of the nerves in this place, since the details are still not clearly enough established to admit of generalizations; but I may devote space for the view to which the embryo and the youngest larval stages of *Petromyzon* have led me. None of my observations contradicts the view, but rather everything indicates that the fibrillæ arise as processes of cells, but not merely from cells of the ganglia and central organ but also from those cells which, ranged in chains, form the first rudiments of peripheral nerves. This being accepted, it appears to me, further, most probable that the growth of the fibrillæ in the dorsal nerves extends in both directions, centripetal as well as centrifugal. Thus, when the rudiments have attained the stage of formation at which they display fibrillæ along with the cells, the cells appear moved apart from each other, and at both ends, the central as well as the peripheral, proceeding forth in fine filaments.

All other questions bearing further upon the peculiarities in this process appear to me at the present not ripe for discussion. Yet I believe I may say one thing definitely, that the rudiments of the dorsal nerves, as well in the earliest phase of the cell chains as also later, when fibrillæ have already appeared, always show the connection with the central organ.

According to what has been hitherto communicated, there enter into the composition of the cranial nerves two systems, the *spinal* and the *branchial*. The first is common to the head and trunk; the latter appears exclusively in the head, is most developed in the fore gill region, and one part is produced into the hind gill region.

Concerning the spinal system of the head, I thus confine myself here to the dorsal rudiments, reserving the ventral spinal nerves for later mention. The complete interruption of the roots between the regions of the trigeminus, acustico-facialis and vagus self-evidently also affects the spinal system. It also divides, therefore, into three regions, of which the hindermost adjoins the spinal system of the trunk. Proceeding from the root-border, the rudiment of a spinal nerve divides into two tracts. The lateral tract (*zug*) remains in connection with the dorsal border of mesoderm—I denote it as the *dorsal branch* of the dorsal spinal nerve—the median tract, or *ventral branch* of the dorsal spinal nerve, passes between mesoderm and brain towards the chorda, passes around this and arrives at the outer side of the aorta. At first consisting of serially arranged cells, this tract includes in itself the rudiments of the *spinal ganglia* and of the *sympathetic ganglia* (Fig. 6).

So far as I have been yet able to discover, the spinal spinal system of the head does not keep pace in further development with the branchial system, but instead undergoes remarkable reductions.

The nerves of the *branchial* system are, in respect to their mode of origin, more composite. The rudiments proceeding

from the root-border grow, with a participation in the principal ganglion then originating, over into the ventral region (Fig. 5, *nb*). It there connects secondarily with a portion proceeding from the distal end of the associated principal ganglion, of which I cannot definitely say whether it is of central or of epidermal derivation—that is to say, whether it is derived from the medial or lateral part of the ganglion, or from both. Then, later, when the epibranchial ganglia arise, further complications ensue. In conjunction with the formation of these ganglia, there appears a peculiar subepidermal layer of cells, which gradually spreads from the eye to the hindermost gill pouch, *but remains confined to the ventral side*.

If it were not preoccupied, I would suggest the name "hypodermis" for this layer, but, as it is, propose the term "neurodermis" (Figs. 6, 7, 10, *nb*). The point of origin of this structure is the vicinity of earliest epibranchial ganglion, dorsad and cephalad of the second gill pouch. At the lateral line, *i.e.*, the outer boundary between the dorsal and ventral region, the neurodermis is not strongly developed; here it consists of several layers of cells which form an inwardly projecting ridge, but in general it remains one-layered and consists of closely arranged but disconnected epithelium-like cells, with a prevailing cylindrical form.

NOTE.—The figures which are referred to in this paper will be collected in plates at the end of the article.

[TO BE CONTINUED.]

## MORPHOLOGY OF THE AVIAN BRAIN.<sup>(1)</sup>

( *Continued.* )

C. H. TURNER.

*Additional Remark upon the External Morphology of the Epencephalon.*—As has been remarked above, the most remarkable characteristic of the avian brain is a tendency towards great compactness. This tendency has left its stamp upon the epencephalon. In addition to being wedged into the caudal V of the hemispheres,<sup>(2)</sup> and to being transversely convoluted,<sup>(3)</sup> the epencephalon suffers a most noteworthy modification. Its cephalo-ventral extremity projects mesad into the cavity of the fourth ventricle, thus producing the almost unique phenomenon of a portion of the epencephalon being embraced by the metencephalon (Plate VII, Fig. 3; Plate XIV, Fig. 10; Plate XV, Fig. 7; Plate XVIII, Figs. 9, 10, 21).

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### V.—HISTOLOGY OF THE EPENCEPHALON.

Although in its external form the avian epencephalon resembles one of the embryonic stages of the higher verte-

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1 A CORRECTION.—Dr. R. W. Shufeldt has called my attention to an error that occurs on page 56, lines 16 to 18. Those lines should read: "My notes upon these two birds are based upon a study of sketches given in the United States Geological Survey, J. W. Powell, Director; third annual report (1881-82), p. 56, Fig. 8, and p. 70, Fig. 20."

2 Supra, p. 41.

3 Supra, p. 51.

brates, yet in its internal structure it differs but little from the adult mammalian cerebellum. As in the mammalia, so here, the epencephalon consists of three major histological regions; the epithelium, the cerebellar cortex, and the body. Around the periphery, lining the convolutions, we find the narrow epithelial layer; entad to this we find the cortex, while further entad, forming the core, we find the body.

*Cerebellar Cortex* (Plate XVIII, Fig. 6).—The transversely and unequally convoluted cerebellar cortex is composed of three laminæ. The most ectal lamina is the widest of all. It is composed of neuroglia through which are scattered a few of Deiter's corpuscles. The second lamina is very narrow. It consists of a single layer of the well-known Purkinje's cells. These are large and gibbous flask cells. In hæmatoxylin and aluminium-sulphate cochineal preparations, these cells are densely stained and present large, clear, spherical nuclei and large, dense nucleoli. In different brains the size of these cells varies greatly, but in all cases they rank with the largest cells in the brain. The width of the next layer is a variable quantity. This dimension varies not only in different brains, but also in different parts of the same epencephalon. But, in every epencephalon, the major local thickenings of this lamina take place in a definite and constant manner. In all cases this layer is narrowest at the proximal extremity of each convolution. Thence the width increases gradually, although irregularly, until the distal extremity of the convolution is reached. There the layer is widest. Although at the proximal extremity of each convolution this layer is often but little wider than the layer of Purkinje's cells, yet at the distal extremity of each convolution it will be almost as wide as the external neuroglia layer (Plate VII, Fig. 4; Plate XIV, Fig. 8). This fact seems to warrant the following suppositions:

1. This layer of the avian epencephalon was deposited before that body became convoluted.



2. Originally this was a uniform layer parallel to the surface of the epencephalon.

3. Its present shape is due to a tendency to remain parallel to the surface which has now become greatly increased by convolutions.

Although the cerebellar cortex is here described as being composed of three distinct layers, it must be borne in mind that neither membranes nor ventricles separate these laminae. Nor is there either membrane or ventricle between the cortex and the remainder of the epencephalon.

*White Substance of the Epencephalon.*—The body or core of the epencephalon is an irregular solid polyhedron, from the periphery of which projections extend into all the irregularities of the ental surface of the cerebellar cortex, and completely fill them. The centre of this core is occupied by a small ventricle, which is connected with the fourth ventricle by a narrow median isthmus. Histologically, this region is composed almost exclusively of fibres. It contains, however, two niduli, one of which is near the ventricle, while the other is in the peduncle.

*Dentate Nidulus.*—The nidulus near the ventricle is large and conspicuous, and is known as the dentate nidulus. It lies, for the most part, cephalad of the ventricle, and is very irregular in outline. In many cases the nerve cells constituting this nidulus are large pyramidal cells, in other cases they are multipolar, while in still others both pyramidal and multipolar cells are found in the same nidulus. In some brains these cells are densely compacted, while in others they are only loosely aggregated. In all cases they lie in a bed of nerve fibres. In my preparations these cells are so densely stained that their nuclei and their nucleoli are invisible. This nidulus is abundantly supplied with Deiter's corpuscles.

## VI.—HISTOLOGY OF THE METENCEPHALON.

*Niduli of the Fifth Nerve.*—The mesencephalic nidulus of the trigeminal nerve has been described in connection with the niduli of the mesencephalon.<sup>(1)</sup> One tract of the fifth nerve arises in the epencephalon, but the niduli of that region also have been described above. There remains then to describe in this connection those niduli only of the trigeminal nerve which are located in the metencephalon.

*Lateral Motor Nidulus of the Fifth Nerve* (Plate XVIII, Figs. 8, 15).—This is a well-defined nidulus which is situated near the lateral surface of the medulla, adjacent to the cephalad root of the trigeminal nerve. Although situated quite near to the lateral surface of the metencephalon, yet it lies entad to that tract of the fifth nerve which passes to the myelon. It also lies cephalad to the tract which passes to the deep motor nidulus of the trigeminus. In different birds the shape of this nidulus undergoes considerable variation. As far as my observations go, the two extremes are represented by the young dove (*Columba livia*) and by the adult Swainson's thrush (*Hylocichla Swainsoni*). In the first case it is a compact spherical nidulus; in the other it is an elongated, straggling nidulus, which lies parallel to the deep motor root of the fifth nerve.

This nidulus is well supplied with large pyramidal nerve cells. The apex of each cell is prolonged into a long process, which process is often curved. In hæmatoxylin and in aluminium-sulphate cochineal preparations, these cells are densely stained, and each one presents a densely stained nucleus and nucleolus. This nidulus is well supplied with Deiters' corpuscles, and nerve fibres traverse it in several directions.

Ventrad to the above nidulus there exists, in some of my sections, an ill-defined cell cluster, which probably deserves

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1 Supra, p. 121; Plate XV, Fig. 3.

to be considered a distinct nidulus. In the medulla of the young dove (*Columba livia*) and in a few other cases this cell cluster appears to be undoubtedly distinct from the lateral motor nidulus of the trigeminus, while in other cases (some of the *Turdidae*) it is evidently amalgamated with that nidulus. Histologically, it could hardly be considered a distinct nidulus. For, although the cells are not typical pyramidal cells, and although they appear to differ from the typical cells of the lateral motor nidulus of the trigeminal nerve, neither are they typical fusiform or flask cells. Although tending towards the flask cells in outline, yet they agree with the pyramidal cells in the structure of their nuclei. In hæmatoxylin and in aluminium-sulphate cochineal preparations, these nuclei are densely stained. After due consideration it has been thought best to consider this cell cluster as a slightly modified portion of the lateral motor nidulus of the trigeminus, which portion occasionally becomes distinct.

*Lateral Sensory Nidulus of the Fifth Nerve* (Plate XVIII, Fig. 8).—This nidulus lies near the lateral surface of the metencephalon, and on the same level as the lateral motor nidulus of the trigeminus. It lies about as near to the lateral surface of the medulla as does the latter nidulus, but it lies upon the opposite side of the deep motor fasciculus of the trigeminal nerve. The form of this nidulus is not constant throughout the class Aves. In some cases (*Hylocichla Swainsoni*) the outline of this nidulus is sub-spherical, while in others (*Columba livia*) it is somewhat irregular. This nidulus is smaller than the lateral motor nidulus of the same nerve.

The cells of this nidulus are flask shaped. In hæmatoxylin and in aluminium-sulphate cochineal preparations, these cells are densely stained, and each one presents a faintly stained nucleus and a densely stained nucleolus. The niduli of these cells are relatively smaller than the niduli of sensory cells usually are. These cells are loosely and irregularly

aggregated, and among them is distributed a large number of Deiter's corpuscles,

*Deep Motor Nidulus of the Fifth Nerve* (Plate XVIII, Fig. 16).—Near the meson, on a level with the niduli of the glosso-pharyngeal and pneumogastric nerves and extending as far cephalad as the roots of the trigeminal nerve, there exists an elongated sub-ellipsoidal nidulus. This small cell cluster lies immediately cephalad of the mesal extremity of the deep motor root of the fifth nerve, and has its major axis approximately parallel to the longitudinal axis of the metencephalon.

The nidulus is composed of a loose aggregate of large pyramidal cells, among which numerous Deiter's corpuscles are distributed. The apex of each cell is prolonged into a long process, while the base is supplied with several shorter processes. The apical process is often curved. In hæmatoxylin and in aluminium-sulphate cochineal preparations, these cells are densely stained, and each one presents a densely stained nucleus and a densely stained nucleolus. Several small fasciculi of nerve fibres pass from this nidulus to the raphe.

In the avian brain there does not appear to be any homologue of what in the human medulla<sup>(1)</sup> is known as the inferior sensory root of the trigeminus.

*Gasserian Ganglion* (Plate XVIII, Figs. 8, 15, 19).—This is a large ganglion which is situated upon the root of the trigeminal nerve. This ganglion consists of large typical bipolar cells, which are arranged with their longitudinal axes perpendicular to the metencephalon. In addition to the ordinary cell wall, each of these cells is surrounded by an additional sheath. In this sheath several nuclei are visible. In hæmatoxylin and in aluminium-sulphate cochineal preparations, these cells are densely stained, and each one presents a faintly stained spherical nucleus, within which is a

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<sup>1</sup> AMBROSE L. RANNEY, "The Applied Anatomy of the Nervous System," second edition, p. 254, Figs. 55, 5.

densely stained nucleolus. From the proximal extremity of each cell a nerve fibre passes into the metencephalon, while from the distal extremity of the same cell a nerve fibre passes into the nerve.

*Nidulus of the Abduçens Nerve* (Plate XVIII, Fig. 10, 13).—This is an ill-defined nidulus which lies near the meson and which extends as far cephalad as the external root of the sixth nerve. In the alligator brain<sup>(1)</sup> and in the human brain<sup>(2)</sup> this cell cluster is situated on the floor of the fourth ventricle. In the avian brain, however, this nidulus is not adjacent to the ventricle, but is separated from it by a large fasciculus of nerve fibres.

This nidulus is composed chiefly of rather small, irregular, pyramidal cells, which resemble those of the niduli of the oculo-motor and pathetic nerves. True, these cells are more irregular than those figured in Plate XVI, Figs. 13, 14; but the cells of the niduli of the third and fourth nerves also are usually more irregular than the cells there delineated. In hæmatoxylin and in aluminium-sulphate cochineal preparations, these cells are usually densely stained, and each cell presents a small densely stained nucleus, within which is a densely stained nucleolus. This nidulus is well supplied with Deiter's corpuscles.

*Niduli of the Facial and of the Auditory Nerves* (Plate XVIII, Figs. 3, 4, 11, 13, 18).—Since in the avian brain the seventh and eighth nerves have a common root, it has been thought wise to describe the niduli pertaining to that root as though they were the niduli of a single mixed nerve. In the avian metencephalon at least three distinct niduli are related to the fibres of facial and auditory nerves. For convenience these are here designated as "nidulus L," "nidulus B," "nidulus Y."

*Nidulus L* (Plate XVIII, Fig. 18).—Far laterad, near the root of the auditory nerve, there is a small sub-spherical

1 PROF. C. L. HERRICK, op. cit., p. 153.

2 PROF. AMERSE L. RANNEY, op. cit., p. 339.



nidulus. The cells of this nidulus are very irregular in outline. They are neither typical pyramidal cells nor typical flask cells. Probably they resemble the former more than they do the latter. In hæmatoxylin and in aluminium-sulphate cochineal preparations, these cells are densely and obscurely stained, and each one presents a densely stained nucleus, within which is a densely stained nucleolus.

The *eminentia acustica* is a slight projection into the cavity of the fourth ventricle. This projection is situated upon the floor of the fourth ventricle, about half way between the external root of the eighth nerve and the meson (Plate XVIII, Fig. 11). This is a sub-elliptical body, and is divided by a band of fibres into two unequal portions. That division which lies nearest the ventricle is much larger than the other portion. This eminentia contains nidulus B.

*Nidulus B* (Plate XVIII, Fig. 18).—As has been mentioned above, this cell cluster constitutes the nervous portion of the eminentia acustica. The band of fibres which divides the eminentia into two unequal portions divides this nidulus in a similar manner. In that section of this nidulus which is nearest the fourth ventricle the nerve cells are crowded into the mesal half, while the remainder of that portion of the nidulus is filled with Deiter's corpuscles. In that section of the nidulus which is on the other side of the band of fibres the nerve cells are uniformly distributed. The cells of this nidulus are small, gibbous, flask cells, which, in hæmatoxylin and in aluminium-sulphate cochineal preparations, are faintly and obscurely stained, and each of which presents a faintly stained nucleus, within which is a densely stained nucleolus. This nidulus is surrounded on all sides by nerve fibres.

It is quite probable that the two divisions of this nidulus correspond to the two small and distinct but adjacent niduli which occupy a similar position in the alligator brain.<sup>(1)</sup>

*Nidulus T* (Plate XVIII, Figs. 4, 11).—Mesad to the

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1 PROF. C. L. HERRICK, "Notes on the Brain of the Alligator," l. cit., p. 153.

above nidulus and between the surface and that tract of the auditory nerve which passes to the raphe, there is an inconspicuous nidulus. This nidulus contains a few scattered fusiform cells and numerous Deiter's corpuscles. In hæmatoxylin and in aluminium-sulphate cochineale preparations, these cells are obscurely stained, and each one presents a faintly stained nucleus, within which is a densely stained nucleolus.

*Root Ganglion of the Auditory Nerve* (Plate XVIII, Figs. 1, 4).—Within the skull cavity the avian eighth nerve bears a small root ganglion. This ganglion is closely appressed upon the metencephalon. Indeed, in some cases it is so intimately connected with the brain that it resembles a superficial nidulus. This ganglion contains large spindle-shaped cells, which apparently are of the same type as those in the Gasserian ganglion. In hæmatoxylin and in aluminium-sulphate cochineal preparations, these cells are densely stained, and each cell presents a faintly stained spherical nucleus, within which is a densely stained nucleolus. Unfortunately, in all my sections that show this ganglion these cells are cut approximately at right angles, thus rendering it impossible to demonstrate whether or not each extremity of the cell is prolonged into a nerve fibre. However, each cell is surrounded by a nuclei-bearing sheath, which resembles the sheaths described and figured for the cells of Gasser's ganglion (Plate XVIII, Fig. 1).

*Nidulus of the Glosso-pharyngeal Nerve* (Plate XVIII, Fig. 16).—At the surface it is almost impossible to distinguish between the roots of the glosso-pharyngeal and pneumogastric nerve, but when we pass into a knowledge of the physiological functions of each nerve renders the separation of the glosso-pharyngeal and pneumogastric niduli an easy matter. Both niduli lie at the meson and in the floor of the fourth ventricle. But the nidulus of the glosso-pharyngeal nerve lies further cephalad and extends farther dorsad than the nidulus of the pneumogastric nerve.

The glosso-pharyngeal nidulus is composed of a close aggregate of small pyramidal cells, among which a few fusiform cells are scattered. The fusiform cells are mostly confined to the caudal portion. The pyramidal cells are quite irregular in outline. In hæmatoxylin and in aluminium-sulphate cochineal preparations, these cells are densely stained, and each one presents a densely stained nucleus, within which is a densely stained nucleolus. This nidulus is abundantly supplied with Deiter's corpuscles.

*Nidulus of the Pneumogastric Nerve* (Plate XVIII, Fig. 16).—Anatomically, the nidulus of the tenth nerve is sometimes distinct from the nidulus of the ninth nerve and sometimes not. Histologically, it is always distinct. It lies caudad to the nidulus of the glosso-pharyngeal nerve, and, usually, does not extend so far dorsad as that nidulus does. Like the above nidulus, the pneumogastric nidulus is elongated, with its major axis parallel to the longitudinal axis of the metencephalon. This nidulus is not quite so wide as the nidulus of the ninth nerve.

The pneumogastric nidulus is composed of large, typical, irregular gibbous cells, which present a strong contrast to the small pyramidal cells of the glosso-pharyngeal nidulus. In hæmatoxylin and in aluminium-sulphate cochineal preparations, these cells are densely stained, and each one presents a large, clearly stained nucleus, within which is a densely stained nucleolus. This nidulus is well supplied with Deiter's corpuscles.

*Nidulus of the Spinal Accessory Nerve* (Plate XVIII, Fig. 16).—Immediately ventrad of the nidulus of the pneumogastric nerve, and extending from the nidulus of the glosso-pharyngeal nerve caudad into the myelon, there is a narrow, elongated cluster of cells. This cell cluster is supposed to be the nidulus of the spinal accessory nerve. This nidulus is composed of large, irregularly arranged, pyramidal cells, which are larger than those of the glosso-pharyngeal nidulus. In hæmatoxylin and in aluminium-sulphate cochi-

neal preparations, these cells are densely stained, and each one presents a densely stained nucleus, within which is a densely stained nucleolus. This nidulus is well supplied with Deiter's corpuscles.

*Nidulus of the Hypoglossal Nerve* (Plate XVIII, Fig. 17).—Further ventrad, and separated from the nidulus of the spinal accessory by a cell-less region, lies the large nidulus of the hypoglossal nerve. This nidulus is sub-pyramidal in shape. Its base is about at the junction of the myelon with the metencephalon, while its apex is as far cephalad as the caudad extremity of the nidulus of the glosso-pharyngeal nerve.

This nidulus is composed of large pyramidal cells, which resemble those of the nidulus of the spinal accessory nerve. In hæmatoxylin and in aluminium-sulphate cochineal preparations, these cells are densely stained, and each one presents a densely stained nucleus, within which is a densely stained nucleolus. This nidulus is well supplied with Deiter's corpuscles.

*Olivæ.*—Near the ventral surface of the metencephalon, and immediately laterad of the root of the hypoglossal nerve, there is a small, ill-defined cluster of cells. This nidulus is probably the homologue of the olivary body. However, this nidulus does not exhibit the slightest trace of the complex structure of the human olivary body.<sup>(1)</sup> The cells of this nidulus are small. In hæmatoxylin and in aluminium-sulphate cochineal preparations, the nuclei of these cells are much more densely stained than is usually the case in flask cells.

*Accessory Olivæ* (Plate XVIII, Fig. 13).—Near the ventral surface of the metencephalon of a young dove (*Columba livia*) a small, ill-defined cell cluster has been observed. It is composed of fusiform cells, and is probably a homologue of the accessory olivæ. In hæmatoxylin preparations these cells are faintly stained, and each one presents a large, clear

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<sup>1</sup> See RANNEY, op. cit., p. 268 and p. 262, Fig. 59.

nucleus, within which is a large, densely stained granular nucleolus.

#### TRACTS OF THE METENCEPHALON.

*Root of the Trigeminal Nerve.*—In the amphibian brain, according to Professor Osborn,<sup>(1)</sup> the fifth nerve root is composed of the following tracts: 1. Ascending tract of the cervical region, reinforced by 2, fibres from the deep motor nidulus, representing two tracts. 3. Fibres from the sensory nidulus. 4. Descending tract from the mesencephalic nidulus. 4. Direct encephalic tract.

In the avian brain the composition of the root of the trigeminal nerve tallies even more closely with the composition of the corresponding nerve of the human metencephalon.<sup>(2)</sup> As in the human brain, so here this nerve is composed of two distinct roots, each of which is composed of several distinct fasciculi. In the lower types of birds (*Columba livia*, etc.) this appearance is quite distinct, but in the higher types (*Hylocichla swainsoni*, etc.) it is often somewhat obscured. One of these roots lies caudad to the other. The cephalad root is composed of two fasciculi, the lateral motor fasciculus and the ascending cervical fasciculus. The caudad root is also composed of two tracts, the lateral sensory fasciculus and the deep motor fasciculus.

*Lateral Motor Fasciculus of the Trigeminal Nerve* (Plate XVIII, Fig. 8). This is a short bundle of loosely aggregated fibres which passes from the lateral motor nidulus of the trigeminal nerve laterad into that nerve. This tract is feebly convex, the convexity projecting caudad.

*Ascending Cervical Fasciculus of the Trigeminal Nerve* (Plate XVIII, Fig. 16).—This is a narrow fasciculus, which, after passing entad for a short distance, turns abruptly and passes caudad into the myelon.

*Lateral Sensory Fasciculus of the Trigeminal Nerve*

1 "Amphibian Brain Studies," Jour. of Morphology, Vol. II, p. 69.

2 See RANNEY'S "Applied Anatomy of the Nervous System," p. 338.



(Plate XVIII, Fig. 8).—This is a small tract which passes from the lateral sensory nidulus of the trigeminal nerve laterad into the root of that nerve.

*Deep Motor Fasciculus of the Trigeminal Nerve* (Plate XVIII, Figs. 8, 15).—This is a broad bundle of fibres which passes from the root of the trigeminal nerve directly mesad to the raphe. It intersects the raphe immediately dorsad of the deep motor nidulus of the fifth nerve. This fasciculus is composed of several narrow, isolated bundles.

In addition to these tracts, there is a tract which descends from the epencephalon and enters one of the roots of the fifth nerve. There appears to be no trace of what Professor Osborn has called the direct encephalic tract, but there appears to be a tract passing into the mesencephalon. Probably that tract communicates with the mesencephalic nidulus of the fifth.

*Tract of the Abducens Nerve* (Plate XV, Fig. 12; Plate XVIII, Figs. 10, 13).—As in the amphibian<sup>(1)</sup> and in the reptilian<sup>(2)</sup> and in the mammalian<sup>(3)</sup> brain, so here, the internal course of the abducens nerve consists of a single narrow fasciculus. This bundle passes from the nidulus of the abducens nerve ventro-laterad to the external root of that nerve. Although small, this tract is relatively larger than the corresponding tract of the mammalian brain.

*Fasciculi of the Facial and Auditory Nerves* (Plate XVIII, Fig. 18).—In birds the root-fibres of the facial and auditory nerves are so intimately associated that it is not now possible to say which fibres belong to the eighth and which to the seventh nerve. In this connection we find four fasciculi,<sup>(4)</sup> one of which passes to the epencephalon. For convenience,

<sup>1</sup> H. F. OSBORN, "Amphibian Brain Studies," p. 70.

<sup>2</sup> C. L. HERRICK, "Notes on the Alligator Brain," p. 153.

<sup>3</sup> AMBROSE L. RANNEY, op. cit., p. 339.

<sup>4</sup> Among my notes I have one, dated several months ago, in which is described for the avian brain a tract resembling the genu of the seventh nerve as it appears in the mammalian brain. Since that time the series that furnished the note has faded so much that verification has been impossible. Other series have been carefully studied, but no such tract has been since encountered.—C. H. T.

the three tracts that are confined to the medulla are designated "tractus L," "tractus B," "tractus D."

*Tractus L.*—This is a short fasciculus which passes from nidulus L directly laterad to the common root of the auditory and facial nerves.

*Tractus B.*—This fasciculus passes direct from the root of the auditory nerve meso-dorsad to the eminentia acustica. There it envelops nidulus B, after which it passes meso-caudad to the raphe. This latter portion of the tract is convex, with the convexity projecting caudad. A similar tract is found in almost all vertebrate brains.

*Tractus D* (Plate XVIII, Fig. 18).—This is a narrow bundle which passes from the common origin of the auditory and facial nerves mesad to the raphe. There it probably decussates. This fasciculus appears to be the homologue of a similar tract discovered by Professor C. L. Herrick in the alligator brain,<sup>(1)</sup> a tract which he considers to be a fasciculus of the facial nerve.

There does not appear to be any very great resemblance between the tracts of the auditory nerve of the birds and the tracts of the corresponding nerve of the amphibia. According to Professor Osborn,<sup>(2)</sup> the eighth nerve of the amphibia is composed of the following tracts: 1. A tract from the posterior longitudinal fasciculus, connecting with the myelon. 2. A tract from a large nucleus situated directly above the exit of the ninth nerve and above the motor nidulus of the trigeminal nerve. (This cell cluster is probably Deiter's nidulus.) 3. A tract from a small group of cells in the lower angle of the metencephalon. 4. A tract from the fasciculus communis. 5. A tract from the epencephalon. Certainly the resemblance is not very striking. Better preparations, however, than those at my disposal might strengthen the homologies between these two groups, for occasionally I have observed a faint indication of what might be a connec-

1 Op. cit., p. 153.

2 "Amphibian Brain Studies," p. 66.

tion between the root of the auditory nerve and the longitudinal fasciculus.

*Fasciculi of the Glosso-pharyngeal and Pneumogastric Nerves.*—The fibres of these nerves pass directly entad to their respective niduli.

*Fasciculi of the Spinal Accessory Nerve.*—The internal root of this nerve consists of a longitudinal series of fasciculi which pass entad from the root to the nidulus of the spinal accessory nerve.

*Fasciculus of the Hypoglossal Nerve.*—This fasciculus passes from its nidulus directly ventro-laterad to its external root.

*Raphe.*—The only commissure in this region is the commissure which connects the two halves of the metencephalon. This commissure extends along almost the entire length of the metencephalon, and is familiarly known as the raphe.

*Crossed Pyramidal Tract.*—The course of this bundle is the same in the avian brain as it is in the human.

*Direct Pyramidal Tract.*—The course of this tract in the avian brain is similar to the corresponding tract of the human. But it is composed of a small fraction only of the median longitudinal fibres that are found near the ventral surface of the medulla. The remainder go to form the dorso-median fasciculus.

*Direct Cerebellar Tract.*—The homologue of this tract is present and has a course similar to its course in the human brain.

*Posterior Longitudinal Fasciculus* (dorso-median fasciculus).—Among anatomists the cephalad terminus of this bundle has long been a open problem. During the past two years two distinguished anatomists, Edinger<sup>(1)</sup> and Honegger,<sup>(2)</sup> have each offered a solution of this problem. Each

1 DR. LUDWIG EDINGER, "Twelve Lectures on the Structure of the Central Nervous System." Trans. by Willis Hall Vittum, M.D., p. 120.

2 JACOB HONEGGER, "Vergleichende Anatomische Untersuchung über den Fornix und die zu ihm Beziehung Gebrachten Gebilde in Gehirns des Menschen und der Säugethiere."

is describing it as it appears in the human subject. Edinger, after remarking that certain of the fibres of the posterior commissure curve caudad, continues: "These fibres, together with others which arise in the depth of the inter-brain, are met with as a fine fasciculus ventrad of the anterior oculo-motor nidulus. As we pass back this fasciculus progressively increases. There are added to it numerous fibres from the nucleus of the oculo-motor. We shall, from now on, meet with the triangular cross-section of this bundle, which is composed of fibres from such various regions on every transverse section of the brain, from the corpora quadrigemina down to the beginning of the spinal cord. This bundle has been called the fasciculus longitudinalis posterior. Inasmuch as fibres are given off along the whole course of this bundle to the nerve-nuclei, as can be plainly seen in embryos of the sixth to seventh month, when few other fibres are medullated, and, as this bundle projects further back than the nucleus of the abducens, it is probable that the fasciculus longitudinalis posterior not only contains the fibres of communication between the nuclei of the ocular muscles, but that it also contains fibres to other cranial nerves. Flechsig is also of this opinion," etc.

Honegger's solution, written contemporaneously, certainly is not in accord with the above. This author considers that this tract does not give off fibres to the posterior commissure. He has also demonstrated that a portion of the fibres of the posterior longitudinal fasciculus pass to the mammillary body, and that other fibres of this bundle decussate in the ventral portion of the diencephalon.

In the avian brain that portion of this fasciculus which lies cephalad of the oculo-motor nidulus consists of a few scattered fibres. Cephalad, these fibres terminate abruptly, near the posterior commissure. Passing caudad, between the oculo-motor and the trochlear niduli, these few fibres become a large bundle. From this point to the myelon there is a progressive increase in the size of this bundle. A short dis-

tance cephalad of the trochlear nidulus the major portion of this fasciculus turns and passes obliquely to the ventral surface of the medulla, thence into the myelon. A few fibres, however, continue caudad and remain near the dorsal surface of the metencephalon. Throughout its course this tract continues near the meson. Although it has not been possible to trace fibres from this fasciculus into any of the niduli of the avian medulla, yet it is evident that fibres are given off all along the line. Although the evidence at hand is not quite conclusive, yet I am inclined to believe the relationship of the avian posterior longitudinal fasciculus is the same as that described above by Edinger for the human posterior longitudinal fasciculus.

*Fibræ Arcuatæ* (Plate XVIII, Fig. 14).—On a level with the auditory nidulus a convex tract, with its convexity projecting laterad, passes from a nidulus in the peduncle of the epencephalon to a nidulus in the ventral portion of the metencephalon.

#### CONCLUDING REMARKS.

1. Economy of space is evidenced in all parts of the avian brain, and the phrase "higher type of birds" carries with it the significance "greater compactness of the brain." Indeed, progressive compactness has played so important a part in the evolution of birds that there is a vast difference between the lowest avian brains, with their large projecting olfactory lobes and exposed optic lobes, and the highest avian brains, with their small, inconspicuous olfactory lobes and covered optic lobes. The difference between these two extremes is almost as great as that between the brain of the lizard and the brain of the lower types of birds. Yet there is no impassable gulf between the brains of the lowest and the brains of the highest types of birds, for all the intervening stages are supplied by the brains of the various avian groups. In reviewing this remarkable sequence, we are almost forced to believe that this tendency towards compactness of the brain



existed long before the first bird was evolved. If this be true, then this tendency towards a progressive compactness of the brain, combined with a tendency to develop all parts pertaining to vision and to atrophy all parts pertaining to smell, will account for all the major differences between the avian and reptilian brain.

Furthermore, within this class of animals, this progressive compactness of the brain is a factor of taxonomic importance. So far, at least, as the major groups are concerned, a classification based upon this alone is in harmony with those classifications that are based upon a study of the structural elements of birds.

2. Neurologically considered, birds are preëminently seeing animals, and all parts that appertain to vision are developed to a great degree. The optic nerve is the largest of all the cranial nerves, and the optic lobes are complexly differentiated bodies. Even the third, fourth and sixth nerves, although quite small, are relatively larger than the corresponding nerves of the mammalian brain.

An extraordinary development of one set of organs is never accomplished but at the expense of some other set. In this case the organs of smell have been the martyrs. Although in the lower avian types the olfactory lobes are paired and conspicuous, yet in the highest type of birds the rhinencephalon is a small unpaired body, which is partly embedded in the base of the cerebrum.

3. Histologically, the avian brain is composed of nerve fibres, nerve cells and neuroglia. In this connection we are concerned with nerve cells only. Although these cells present a great diversity of forms, yet they may all be grouped in the following classes: ganglionic cells, Deiter's corpuscles, fusiform or flask cells, pyramidal cells, and multipolar cells. The ganglionic cells are large bipolar cells, which are never found outside of the root ganglia. Each extremity of each of these cells is prolonged into a nerve fibre. In addition to the ordinary cell wall, each cell is surrounded by a special,

nuclei-bearing sheath. Deiter's corpuscles are small cells, which contain so small an amount of protoplasm that ordinary preparations reveal only their nuclei. These minute cells are universally distributed. The remaining three types are encountered throughout the brain; but in any one nidulus some one type always predominates, often to the exclusion of the other two. The flask cells resemble a flask in shape, and when stained each cell presents a faintly stained nucleus, within which is a densely stained nucleolus. Such cells are supposed to be sensory in function. The pyramidal cells are sub-pyramidal in outline. These cells stain densely, when each one presents a densely stained nucleus, within which is a densely stained nucleolus. Such cells are probably motor in function. The multipolar cells resemble distorted, many-branched pyramidal cells. Such cells probably act as switch stations for nervous energy.

#### EXPLANATION OF PLATE XVIII.

*Fig. 1.* Transverse section of the brain of *Hylocichla Swainsona*, taken through the root ganglion of the auditory nerve; *a*, tractus B of the seventh and eighth nerves; *B*, nidulus B of the seventh and eighth nerves; *d*, nidulus d of the seventh and eighth nerves; *sg*, root ganglion of the auditory nerve.

*Figs. 2, 3, 4, 5.* Transverse section of the metencephalon of *Sialia sialis*; *V*, root of fifth nerve; *VIII*, root of seventh and eighth nerve.

*Fig. 6.* Section through the cortex of the epencephalon.

*Fig. 8.* Horizontal-longitudinal section through the fifth nerve root of *Hylocichla Swainsoni*; *IV*, root of trochlear nerve; *V*<sup>3</sup>, lateral sensory root of the trigeminal nerve; *5*<sup>1</sup>, lateral motor nidulus of the trigeminal nerve; *5*<sup>3</sup>, lateral sensory nidulus of the trigeminal nerve.

*Fig. 9.* Horizontal longitudinal section through the metencephalon of the domestic turkey brain, taken through the tenth nerve root; *X*, tenth nerve root; *9*, nidulus of the ninth nerve; *10*, nidulus of tenth nerve.

*Figs. 10-12.* Successive transverse sections of the metencephalon of *Hylocichla Swainsoni*; *a*, tractus B of the auditory nerve; *B*, nidulus B of the seventh and eighth nerves; *d*, nidulus Y of the seventh and eighth nerves; *V*, root of the trigeminal nerve; *VI*, root of the abducens nerve; *7*<sup>1</sup>, nidulus B of the seventh and eighth nerves; *9*, nidulus of the ninth nerve.

*Figs. 13-14.* Transverse section through the metencephalon of

*Columba livia* (nestling); *A. O.*, accessory olives; *F. a.*, Fibræ arcuatæ; *VII*, root of abducens nerve; *VIII*, root of seventh and eighth nerves.

*Fig. 15-17.* Horizontal longitudinal sections of the metencephalon of *Columba livia*: *Va*, lateral motor fasciculus of the trigeminal nerve; *Vb*, deep motor fasciculus of do; *Vc*, cervical fasciculus of do; *IX*, root of ninth nerve; *X*, root of tenth nerve; *5*, deep motor nidulus of the trigeminal nerve; *11*, nidulus of the eleventh nerve.

*Fig. 18.* Transverse section through the metencephalon of *Agelæus phœniceus*, taken through the root of the auditory nerve; *VII*, tractus d of the seventh and eighth nerves.

*Fig. 19.* Cells from the Gasserian ganglion of *Hylocichla Swainsoni*.

*Fig. 20.* Diagram illustrating the course of a few of the tracts of metencephalon. No attempt has been made to represent the relative thickness of the tracts; *A. C.*, anterior commissure; *A. P.*, anterior peduncle of the cerebellum; *C. C.*, corpus callosum; *C. S.*, commissura sylvii; *D. C.*, direct cerebellar tract; *L. F.*, posterior longitudinal fasciculus; *P. C.*, posterior commissure. *P. F.*, pons fibres (these are very few and scattered); *P. N.*, peduncular nidulus; *P. T.*, pyramidal tracts; *T. E.*, tract from the epencephalon (see p. 125); *T. T.*, tænia thalami. Roman numerals indicate the corresponding nerve niduli.

*Fig. 21.* Diagram illustrating the course of a few tracts of the metencephalon. No attempt is made to represent the relative size of the tracts; *C. g.*, corpus geniculatum externum; *c. n.*, crescent-shape nidulus; *c. p.*, crossed pyramidal tracts; *D. P.*, direct pyramidal tracts; *I. C.*, inferior commissure; *M. V.*, mesencephalic ventricle; *N. p.*, nucleus posterior; *P. g.*, prosencephalic tract from the corpus geniculatum; *P. N.*, nidulus pyriformis and nidulus lenticularis; *P. V.*, prosencephalic ventricle; *T. B.*, Tractus Bummi. Roman numerals indicate the corresponding nerve tracts. Arabic numerals indicate the corresponding nerve niduli.

*Fig. 22.* Transverse section of the brain of *Sialia sialis*.

*Fig. 23.* Cells from lateral sensory nidulus of the trigeminal nerve of *Columba livia* (nestling).

*Fig. 24.* Cells from lateral motor nidulus of the trigeminal nerve of *Columba livia* (nestling).

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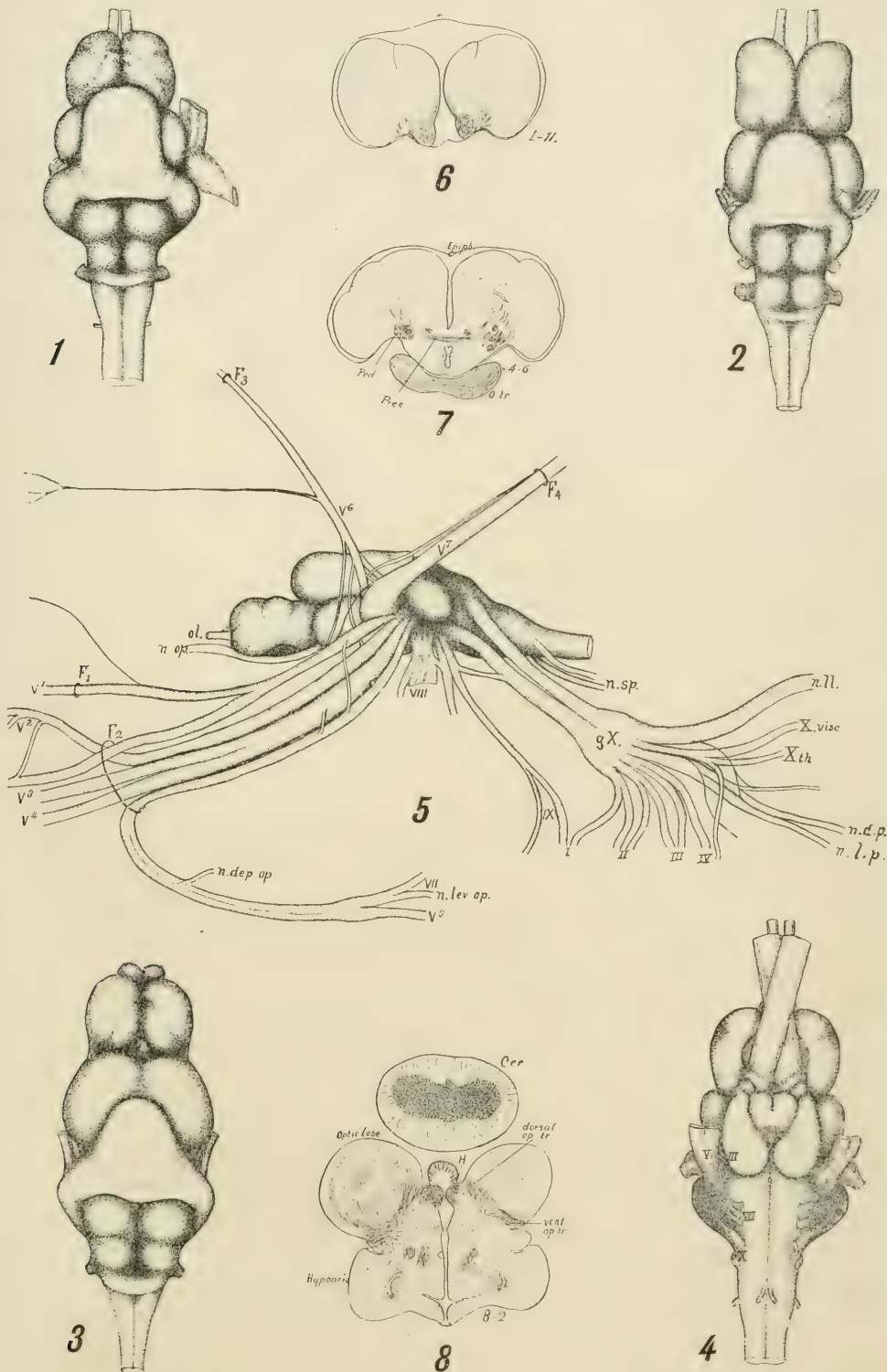
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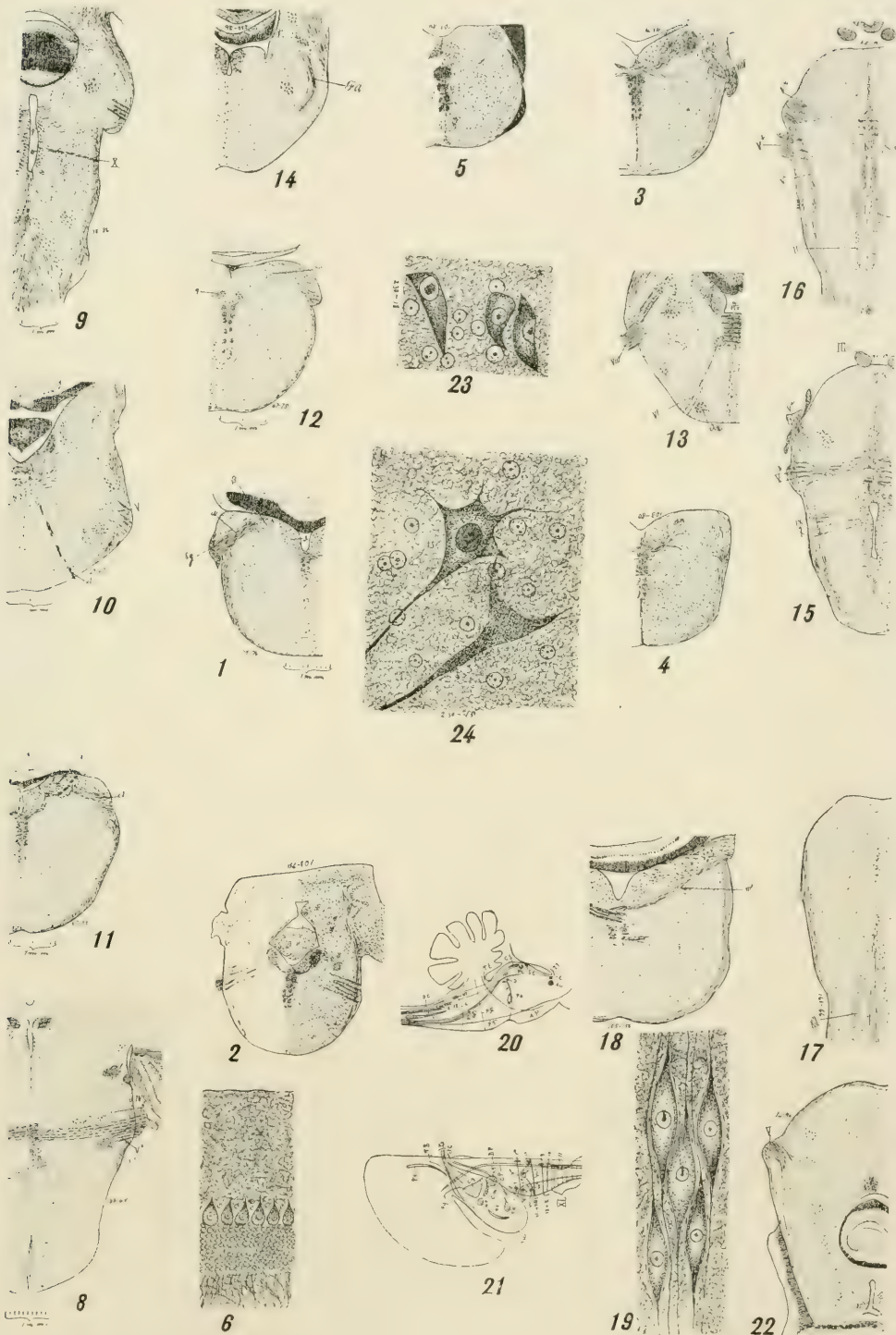
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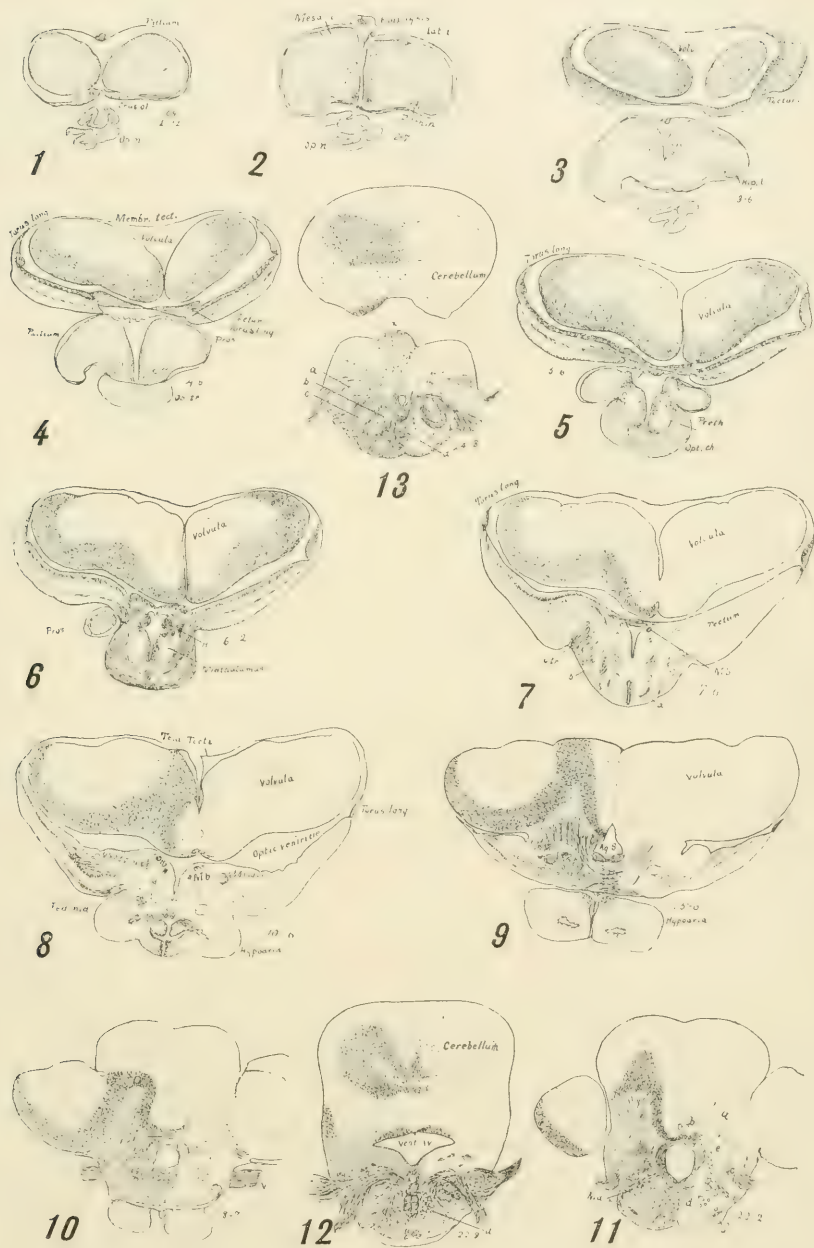




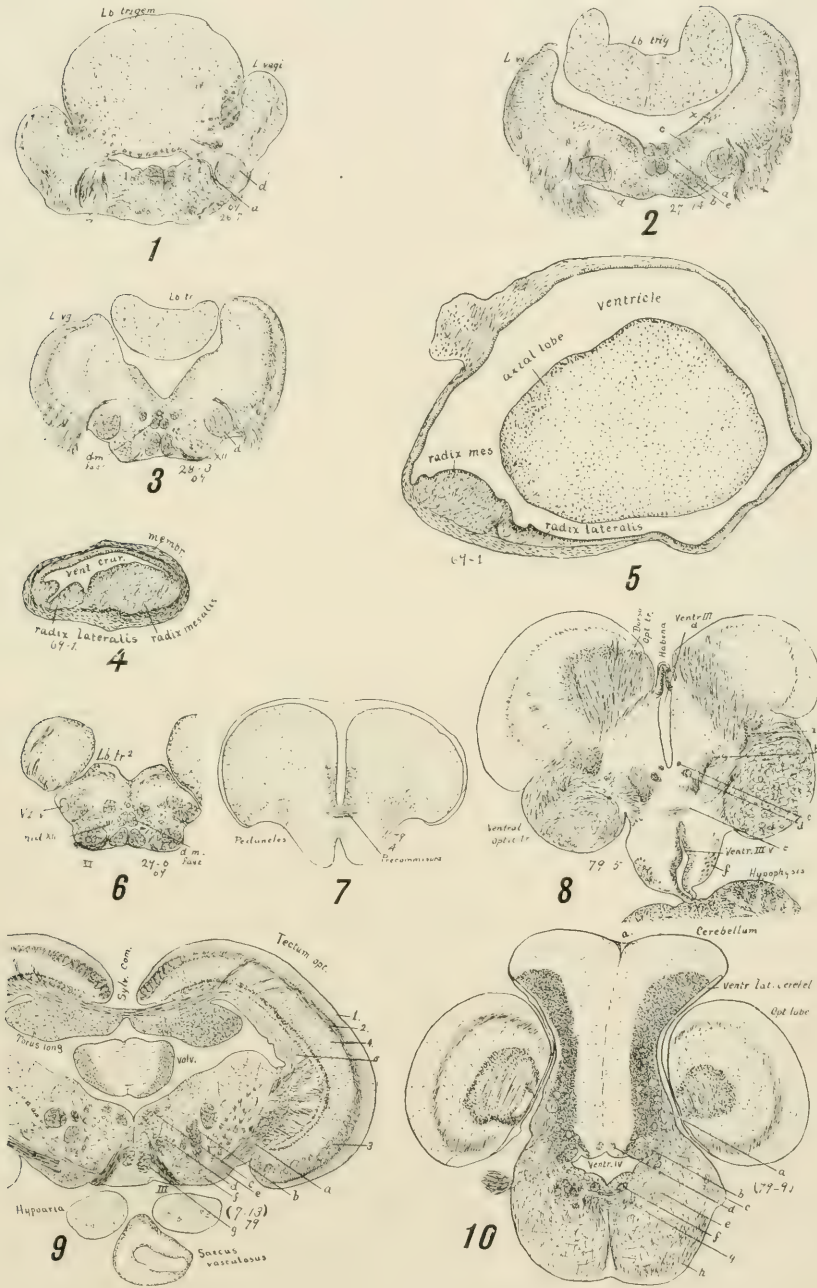
















## THE LUMBAR, THE SACRAL, AND THE COCCY- GEAL NERVES IN THE DOMESTIC CAT.

With Plate XXIII.

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The present contribution to comparative neurology is offered in the hope that it may serve as a factor to strengthen the argument in favor of the substitution of comparative anatomy for anthropotomy in the first year's work of our medical courses, and also to justify the practice of callisection or painless physiological experimentation. The constancy of character, *i.e.*, the slight variation in nerve ramuli and their distribution, seems to favor making neurology the basis of comparative anatomy, rather than osteology or myology. Believing such to be the case, it is hoped that this study may prove helpful in establishing doubtful homologies. If the educational or cultural in contradistinction to the utilitarian view of the subject be considered, there seems abundant demand for the work undertaken by the paper as a guide to laboratory students with whom the end is general and not specific. For it is quite generally conceded that comparative anatomy furnishes one of the most available means for training the perceptive activities as well as those of comparison and induction. Furthermore, physiology is almost wholly a comparative science; while some of the facts known to physiology have followed direct experiment, the great majority are the results of partial experimentation upon other mammals. It needs no proof beyond mention to show

that the present plan of study in the medical college is not as extensive as it should be to furnish the technical skill and exact knowledge which the profession demands. That human physiology is largely comparative will be readily admitted, but unless the student knows that the structures in the animal experimented upon are strictly homologous with the structures in man the physiological experiment becomes merely an illustrative exercise, interesting and instructive, but not a demonstration of function in man.

When it is shown that the nerve-supply is identical with the nerve-supply in man, then these experiments in which the nervous system is a controlling factor are conclusive evidence in human physiology also; *e.g.*, at this moment my mind selects the elaborate experiments of Dr. H. P. Bowditch upon the vaso-motor nerves, the results of which were presented before Section F, A. A. A. S., Buffalo meeting, 1886.

Among reasons for the selection of a small mammal may be named the cost and convenience of suitable preparation, preservation and manipulation. In regard to cost, it should be remembered that for exact work each individual should dissect an entire body—the reserve half serving for corroboration, verification, correction of errors from accident or oversight, study of variations in the same individual, etc. The writer found it a matter of no small expense and labor to prepare and to preserve in alcohol the adult cadavers which formed the basis of his studies in anthropotomy; the convenience of manipulation will be appreciated by those who have had the experience of transferring a large adult cadaver from tank to table.

The adaptation of the domestic cat to the ends sought (comparative neurology) may be briefly stated as follows:

1. The readiness with which structures may be homologized with corresponding structures in man (certain nerves in the dog are quite unlike those in man, *e.g.*, vagi). That there are marked differences between the human brain and

other mammalian brains is generally known, and possibly some other animal is preferable to the cat as a type for this portion of the neur-axis.

2. The abundance of material for study.

3. The inexpensiveness of (*a*) the body; (*b*) of suitable preparation of the same, injection, etc.; (*c*) of preservation of the same.

4. The ease of manipulation; the tissues are much firmer than they are in a small human subject, fœtus or infant.

To these more apparent considerations may be added the fact that already elaborate works on felitomy are accessible, *e.g.*, Straus-Durckheim's monogram on the "Skeleton Ligaments and Muscles of the Cat" ("Anatomie du Chat," two vols.), or the less expensive reduced copies with "Explanations" by Prof. H. S. Williams; St. George Mivart's "The Cat," although this work does not seem to be a reliable guide to the study of American cats; the more scientific and exact work of Wilder and Gage, entitled "Anatomical Technology," and the numerous papers and addresses of the same authors, a partial list of which is found in the work cited; and the papers embodying some of the writer's studies in comparative neurology.<sup>(1)</sup>

#### PREPARATION.

The cats were killed with chloroform and both arteries and veins were injected with the *starch injection mass*. When not in use the body was wrapped in a napkin saturated with alcohol and then placed in a tight vessel; the tissues are by this means preserved in excellent condition.

#### GENERAL DESCRIPTION.

The myel may be regarded anatomically as an elongated mass of alba and cinerea, and functionally as an aggregation

<sup>1</sup> "The Vagus Nerves in the Domestic Cat:" The Trigeminus, The Facial, The Glosso-pharyngeal, The Accessory, The Hypoglossal, The Soft Palate. The literature of the subject was cited in a paper read before the American Philosophical Society, May 21, 1886.

of sensory and motor centres especially characterized by reflex action. Corresponding to its relations with the vertebræ, it is usually divided into the five regions, *cervical*, *thoracic*, *lumbar*, *sacral*, and *coccygeal*; and the myelic nerves are named from the vertebræ cephalad of which they have their respective ectal origins. The lumbar and the sacral nerves form open plexuses (Pl. lumbalis and Pl. sacralis), from which nerves are distributed to the integument and the subjacent muscles.

#### POSTURE.

Ventri-cumbent, head toward dissector's left, or lateri-cumbent, with the venter toward the dissector.

#### EXPOSURE.

It is not imperative that the dissection begin at any particular point, but most of the nerves send branches caudad rather than cephalad (v. diagram), hence it is recommended to begin at the thirteenth thoracic nerve and dissect caudad, removing the neural arch and exposing the myel as the dissection progresses. Make a long incision through the integument about 2 cm. sinistrad of the dorsi-meson, from the tenth thoracic vertebra to the base of the tail. From the cephalic end of this incision make a second incision ventrad 4-6 cm., and reflect the flap of integument over the twelfth and thirteenth ribs. With the arthrotome remove the dorsal muscle from the sinistral side of the meson to the level of the vertebral laminæ of the twelfth and the thirteenth thoracic vertebræ. With the tracer find the thirteenth thoracic and the first lumbar nerves just peripherad of the vertebræ, trace them centrad to the foramina intervertebrales, separate the connecting tissues from the foramina, then with the side-cutting nippers remove the neural arch of the thirteenth thoracic vertebra, taking the precaution to make the first incision near the neurapophysis, to insure protection to the myel. The dextral lamina can be removed without injury to

the dorsal muscles or integument, making it possible to use the dextral side to corroborate and to correct results obtained by dissecting the sinistral. The exposure of the myel in the arch of the caudal thoracic vertebra (thirteenth) exposes the ectal origin of the first lumbar nerve. The arch can be removed in a similar manner caudad and dextrad as the dissection requires, using the precaution to trace the dorsal division of each nerve before removal of the dorsal muscle. The nerves should be traced from the ectal origin peripherad.

#### LUMBAR NERVES. NERVI LUMBALES.

*Common Characters.*—The lumbar nerves are seven pairs, and have characters in common. They are related with the sympathetic system by anastomotic filaments to the adjacent ganglia (Fig. Pl. S. and S.), which filaments leave the ental surface of the nerve as it traverses the groove from the neural arch to the inter-vertebral foramen (foramen of exit); these anastomotic filaments are apposed to an arteriole—the dorsal branch of the A. lumbalis. At the ectal border of the foramen of exit, each nerve divides into a dorsal and ventral portion; the dorsal nerve divides into two or more branches, which innerve the muscles of the back (MM. quadratus lumborum, erector spinæ, intervertebrales) (Fig. M. dor.), which are especially large in the cat. A branch from each dorsal nerve can be traced to the integument (Fig. Int.), where it joins in an open plexus with the adjacent nerves.

The nerve trunk or ventral division dips ventrad close to the border of the centrum and mesad of the diapophysis; the origin is thus concealed by fascia, aponeuroses and superposed muscles. At the ventral border of the centrum the nerve usually passes laterad (except the branch to form the lumbar plexus) apposed to the abdominal branch of the lumbar artery. From the ental surface of the trunk adjacent to the centrum a branch is given off which separates into three to five ramuli to the proximal or aponeurotic portions of the M. psoas (Fig. Pso.), and two anastomotic rami to the sym-



pathic ganglia (Fig. S.) cephalad and caudad; in the cephalic three lumbar nerves, these rami join the great solar plexus (Fig. Pl. S.).

The lumbar nerves are conveniently grouped into two groups, those which do not enter into the lumbar plexus, viz., *the cephalic four pairs*, comparable with the first lumbar (anthropotomy), and those which are so related, viz., *the caudal three pairs*, comparable with the lower four lumbar nerves (anthropotomy).

*Special Characters.*—*The first and second lumbar nerves* give the first branch to the diaphragm (Fig. Dia.) instead of the M. psoas; they join the solar plexus (Pl. S.), they follow the abdominal lumbar artery through the aponeurotic origin fibres of the diaphragm, and lie upon its cephalic surface 25 mm. peripherad of the foramen of exit. Five mm. still peripherad, in the aponeurotic interdigitations of the ectal oblique muscle (M. abdominis obliquus ectalis), the trunk separates into cephalic (Fig. ce.) and caudal (Fig. ca.) divisions. *The cephalic division* follows the abdominal artery, penetrates the overlying (ectal) muscle, innerves the ental, the transverse and the rectus muscles of the abdomen, anastomoses with the cephalic divisions of the adjacent nerves (Fig. anas.), and sends terminal filaments to the adjacent integument (umbilical and hypogastric). *The caudal division* has its course caudad and slightly ventrad; it lies upon the ectal surface of the ental muscle, to which it gives filaments in the umbilical and the hypogastric regions. This division lies entad of the cephalic division of the lumbar nerve next caudad.

*The third and fourth lumbar nerves* (first lumbar of anthropotomy). These nerves have the ectal origins and proximal rami similar to the first and second. The third nerve joins the solar plexus cephalad, but the sympathetic ganglion caudad. The fourth does not anastomose with the plexus. *The cephalic divisions* are distributed farther caudad, reaching the gluteal (Fig. Th.) and inguinal regions (Fig.

Pub.), and giving numerous filaments in plexiform relations over the hypogastric integument. *The caudal division* of the third lies entad of the cephalic division of the fourth, and ectad of the cephalic ramus of the ilio-lumbar artery; 20 mm. from its origin it crosses a ramulus of the caudal ramus of the same artery as the arteriole perforates the lateral border of the M. abdominis rectus. The nerve gives filaments to the transverse (Fig. trans.) and to the ental oblique (Fig. M. ent.) muscles. *The caudal division* of the fourth lies apposed to the caudal ramus of the ilio-lumbar artery for 15–20 mm.; it passes between the cephalic and the caudal divisions of the genito-crural nerve. It innerves the transverse and ental muscles 10–15 mm. dorsad of the region supplied by the caudal division of the third, and terminates in the rectus abdominis muscle.

*The fifth, sixth and seventh lumbar nerves* are distinguished from the other lumbar nerves by the plexus (Pl. lumbalis) formed by the dorsal or caudal divisions of the ventral nerve trunks. These nerves rapidly increase in size, the seventh being considerably the largest. The union of the divisions or branches just ventrad of the vertebral diapophyses forms not only an important part of the lumbar plexus, but constitutes the lumbo-sacral cord of anthropotomy, from which nerves take their ectal origins, v. below.

N. GENITO-CRURALIS, N. LUMBO-INGUINALIS; N. PUDENDUS  
EXTERNUS.

The genito-crural nerve (second lumbar of anthropotomy) has its ectal origin by two roots; the cephalic root seems to be the lateral continuation of the fifth lumbar nerve, the caudal root is a large branch of the sixth lumbar nerve, given off at the foramen of exit centrad of the plexus. The root nerves are inter-related by anastomotic filaments. The trunk formed by the union of the roots penetrates the aponeurosis of the M. psoas, lies upon its ectal surface about 2 mm. laterad of the mesal border of the muscle, and separates into

two divisions, cephalic and caudal. *The cephalic division, the crural branch* (crur.), bends around the lateral border of the M. psoas, and 20 mm. peripherad of its origin it accompanies the ilio-lumbar artery into the transverse muscle. Its course is caudad in the transverse and ectal muscles, and leaves the pelvis by the ectal abdominal ring entad of Poupart's ligament; its course outside the pelvis is along the ectal fascia over the caudal thigh to the knee, and terminates in the integument of the proximal crus, where it joins filaments of the external cutaneous nerve. *The caudal or dorsal division, the genital branch* (gen.) lies upon the meso-ental surface or border of the M. psoas, entad of the ilio-lumbar artery, at which point it gives a large anastomotic branch to the open plexus of nerves and vessels of that region, and thence continues caudad in the ental muscle, to which it gives several filaments. At the Poupart's ligament (Fig. P.) it is reflected ventro-cephalad, and terminates in the integument of the hypogastric region; filaments from the point of reflection extend to the integument over the pubes. (I have not traced this nerve in the male.)

#### N. CUTANEUS ECTALIS.

The external cutaneous nerve (Ext. Cut.) has its ectal origin by two roots; the cephalic root is a branch of the loop (Fig. Loop) between the fifth and the sixth lumbar nerves; the caudal root is a branch of the sixth nerve in common with the caudal root of the genito-crural. The origin and the distribution of the genito-crural and the external cutaneous nerves indicate an intimate inter-relation.

The course of the nerve lies ectad of the anastomotic branch from the G. sympathicus to the sixth lumbar nerve; it runs obliquely through the origin fibres of the M. psoas and comes to superficial view at the mesal border of that muscle at the point where the iliac artery lies apposed to the aponeurosis of the M. psoas, about 20-30 mm. cephalad of the ramus of the pubis. Exposure is readily made by

tracing the mesal border of the M. psoas caudad from this point.

The nerve lies ectad (ventrad) of the external iliac artery and vein, and entad of the common iliac vein which is ventrad of and apposed to the artery; it bends around the artery and lies upon its ental surface, ectad (ventrad) of the hypogastric artery just cephalad of the ramus pubis.

It leaves the pelvis through the abdominal ring, 20 mm. peripherad of which it separates into two divisions, one of which (Fig. ce.) is distributed to the integument of the hip (Fig. H.) and the proximal half of the caudal thigh (Fig. Th); the other division (Fig. ca.) is distributed to the integument over the biceps muscle as far as the knee. The nerve was wanting on the sinistral side of one specimen (female).

#### N. CRURÆUS ANTERIOR.

The anterior crural (Ant. Crur.), the seventh lumbar nerve, is the largest of the spinal nerves whose origin is not referable to the union of two or more nerve trunks. It supplies *muscular* branches to the psoas, the iliacus, the sartorius, the pectineus muscles and the muscles of the cephalic (inner) thigh except the tensor vaginæ femoris, which is innerved by a slender ramus of the superior gluteal nerve (q. v.); and *cutaneous* branches to the integument of the thigh, the leg, the cephalic part of the foot and the plantar surface of the toes.

The seventh lumbar nerve at the foramen of exit sends anastomotic branches to the adjacent sympathetic ganglia; its dorsal division innerves the muscles of the back (Fig. M. dor.) and the adjacent integument (Fig. Int.); the large ventral division (2 mm. in section) lies close to the lateral surface of the centrum and at its ventral border receives the large trunk (Fig. L. S. C.) of the sixth lumbar nerve, and sends an equally large trunk caudad (Fig. L. S. C., lumbosacral cord of anthropotomy) to the first sacral nerve.

*Origin.*—The anterior crural nerve is the ventral division of the seventh lumbar, of which it is strictly the continuation with a large accession from the sixth—or its origin may be referred to the lumbar plexus.

*Principal Rami.*—The ectal origin of the nerve lies entad of the M. psoas, to which several filaments are given (Fig. Pso.) 2 mm. peripherad of its origin; 5 mm. peripherad a large branch is given caudad to the M. iliacus (Fig. M. il.). The general course of the nerve trunk is embraced by the M. psoas, the nerve reaching the ectal surface or lateral border of the muscle in the region of the iliac notch, or 20 mm. ventro-caudad of its origin. Entad of Poupart's ligament (Fig. P.) it gives from its lateral border a large ramus which innerves the sartorius muscle (Fig. Sar.), which ramus lies entad of a ramus of the profund artery 10 mm. from its origin. As the nerve crosses the artery a slender branch passes ectad of the artery to the mesal border of the sartorius muscle. The larger portion of this branch lies upon the ental surface of the muscle, and can be traced to its distal extremity or insertion, thus innerving its distal three-fourths; the smaller portion of the nerve is reflected proximad at the profund artery, and innerves the proximal (origin) one-fourth of the sartorius muscle, lying upon its ental surface.

Entad of Poupart's ligament and 2 mm. peripherad of the sartorial branch, from the mesal border of the nerve is the ectal origin of the long saphenous nerve (N. cutaneus internus longus, Fig. Saph. l.).

#### THE LONG SAPHENOUS NERVE.

This nerve lies ectad of the femoral artery and apposed to it and the long saphenous vein, the vein being mesad, the artery in the middle, and the nerve laterad upon the surface of the thigh.

*Principal Rami.*—The first branch is given to the artery (Fig. A. fem.). At the knee (Fig. K.) two ramuli are given off; the *lateral* ramulus (Fig. l. r.) is cutaneous; it accom-



panies an arteriole and is distributed to the integument over the cephalic surface of the proximal third of the crus; the *mesal* ramulus (Fig. m. r.) lies ectad of the artery and vein and is distributed to the integument mesad of the vein, its terminal filaments anastomosing with other filaments of the nerve trunk. Below the knee (Fig. K.) (upon the crus) the nerve continues as two divisions corresponding with the two arteries, with whose courses they are nearly parallel; the *lateral division* is distributed to the integument over the cephalic surface of the distal half of the crus and the 'pes; the *mesal division* lies in the fascia ectad of the tibia; its course is just mesad of (behind) the cephalic malleolus, ectad of the tendon of the M. tibialis anticus; it forms a dense plexus upon the cephalic metatarsale (2) and joins the plantar plexus (Fig. Pl. Plan.), its terminal filaments being traceable to the distal extremities of the toes and to the plantar pads.

*The muscular division* (deep layer of anthropotomy) of the anterior crural nerve, near its origin at Poupart's ligament, follows the profund artery, dips entad in Scarpa's triangle, and gives a branch to the M. sartorius (Fig. Sar.), which branch, 5 mm. peripherad (at the border of the M. rectus femoris), lies entad of the artery and separates into a peripheral and a central portion; the peripheral branch may be traced in pinniform arrangement throughout the distal three-fourths of the muscle to the knee; the central branch is reflected at the artery and is distributed to the proximal fourth of the muscle.

At the origin of the last branch the nerve penetrates the M. rectus femoris (Fig. M. r. fem.), to which three rami are given. The proximal ramus innerves the proximal third of the muscle, the second lies upon the ental surface of the muscle and innerves its distal two-thirds, to the insertion at the patella; the third ramus enters the caudal border of the muscle near its middle. These three rami are motor. Five mm. peripherad of the branch to the M. sartorius a ramus is

given to the M. vastus internus (V. int.) and to the M. crureus. At the caudal border of the M. vastus internus filaments are given to the muscle; the nerve lies entad of the M. rectus femoris and the adjacent M. vastus externus, whose ental surface it penetrates, accompanied by an artery, and distributes filaments from three ramuli to the M. vastus externus. The nerve can be traced around the lateral border of the femur with the internal circumflex (?) artery into the M. pectineus.

#### N. OBTURATOR.

*Origin.*—The obturator nerve (N. Obt.) has its ectal origin from the lumbo-sacral cord between the seventh lumbar and first sacral nerves, 16 mm. caudad of the anterior crural nerve; in one specimen the origin was by the union of a lumbar (seventh) and a sacral (first) root at the ventral border of the ilium. Its course is caudad, ectad of the ental iliac artery and ventro-mesad of the ventral border of the ilium; it pierces the obturator muscle 30 mm. caudad of the origin of the nerve; it leaves the pelvis through the Fm. obturator, peripherad of which it divides into several rami.

*Principal Rami.*—The first ramus (N. obturator accessorius (?)) is directed ectad to the superposed M. pectineus (Fig. M. Pec.). A long ramus bends over the cephalic surface of the origin of the adductor muscle, lies upon the ental surface of the M. gracilis apposed to an arteriole, and innerves the gracilis (Fig. M. grac.), in which muscle it may be traced to its aponeurotic insertion at the knee, centrad of which anastomotic filaments relate it with the long saphenous nerve.

Four rami lie upon the ectal surface of the proximal end of the adductor muscles (MM. magnus and brevis), just peripherad of the foramen, in which muscles they terminate.

Entad of the M. adductor longus, between it and the M. adductor brevis, two ramuli cross the M. adductor brevis and are distributed to the M. adductor magnus, attended by rami

of the internal iliac artery. Terminal ramuli like a leash supply the M. adductor longus and the M. obturator externus.

#### SACRAL NERVES.

*General Description.*—The sacral vertebræ are three, and the nerves are corresponding three pairs. These nerves are characterized by the length of the ectal roots and by the distance through which they are traced in the neural arch and in the groove from the arch to the intervertebral foramina. At their respective foramina of exit they separate into two unequal divisions, the dorsal and the ventral; *the dorsal division* passes directly dorsad and divides into cephalic and caudal rami, each of which anastomoses with the terminal filaments of the adjacent nerves, and each sends a considerable branch to the open plexus of cutaneous nerves; *the ventral division* passes directly ventrad and laterad to join in the formation of the sacral plexus, from which nerves are distributed to the caudal extremity. Each ventral nerve receives an anastomotic nerve from the adjacent sympathetic ganglia (Fig. S.).

#### THE FIRST SACRAL NERVE.


*Special Description.*—The first sacral nerve is the largest of the spinal nerves, and has its ectal origin in the neural arch of the sixth lumbar vertebra, at the caudal border of which may be found its dorsal root ganglion; it traverses the long groove (10 mm.) in the seventh lumbar vertebra, and finds its exit through the foramen mesad of the crista ilii and ventro-mesad of the broad diapophysis of the first sacral vertebra. Immediately peripherad of the foramen of exit it is joined by the lumbo-sacral cord (Fig. L.-S. C.)—which in a medium-sized cat is 2 mm. in section—and has its course mesad and ventrad of the diapophysis and the crista ilii, by which it is concealed, and which renders its exposure somewhat difficult. The nerve trunk at this point (its central 10 mm.) is about 4 mm. in section.

*Principal Rami.*—The first nerve from the sacral plexus, *N. Gemellus* (Fig. Gem.), is given from the ectal surface of the first sacral nerve where it is joined by the lumbo-sacral cord (Fig. L.-S. C.) at the caudal border of the first sacral vertebra, and is directed dorsad; it lies close to the vertebra for its central 5 mm., and then passes laterad into the gemellus muscle, and is distributed by three branches. This muscle has its origin along the sacral vertebræ, but its relation with the *M. gluteus maximus* and its insertion with the *M. obturator internus*, as well as the innervation, lead to its identification as the *M. gemellus superior*.

From the cephalic border of the first sacral nerve a branch is sent laterad and around the ramus of the ilium cephalad of the acetabulum to the *M. pyriformis* (Fig. Pyr.). The nerve trunk lies ectad of the sacral artery and vein, and leaves the pelvis through the great sciatic foramen upon the ectal surface of the *M. quadratus femoris*, the *M. obturator* and the *M. pyriformis*, and entad of the *MM. glutei*.

About 10 mm. caudad of the foramen of exit a branch from the ental surface is given to the *M. gluteus maximus* (Fig. M. gl. max.), and 5 mm. still peripherad a branch caudad and entad of the *M. obturator internus* (*M. obt. in.*), which branch divides into two rami, the shorter being distributed to the overlying obturator and the longer terminating in the quadratus muscles. The nerve to the *M. gluteus* is sometimes a branch from the second sacral nerve (see Fig. F).

#### THE SECOND SACRAL NERVE.

The ventral division of this nerve is much smaller than the first sacral nerve; it takes a ventro-laterad course, and joins the first sacral just mesad of the trochanter. The union of these two trunks constitutes the great sciatic nerve  *q. v.*

*Principal Rami.*—The dorsal division is already described in common with the other sacral nerves, v. "General Description." Its caudal branch joins the plexus which innerves

the dorsal muscles and the integument of the tail. A large anastomotic *loop* joins the *ventral division* of the third sacral nerve just peripherad of the foramen of exit. A slender branch is sometimes given as a distinct nerve to the overlying M. gluteus maximus (Fig. M. gl. max.).

#### THE THIRD SACRAL NERVE.

*The ventral division* is the smallest of the sacral nerves; it divides into ental and ectal branches. *The ental or deep branch* lies upon the ectal surface of the long levator ani muscle (Fig. L. A.), to which it is distributed. *The ectal branch* joins the second sacral nerve in a large anastomotic branch or *loop*, and peripherad of this a smaller loop joins the first coccygeal nerve (Fig. N. Coc.) and at the same point gives off the second root of the N. coccygeus (Fig. N. Coc.).

*Principal Rami.*—The nerve trunk divides into three branches, which lie entad of the rami to the M. gluteus maximus and the M. obturator internus, already described. *The cephalic branch* joins the N. ischiadicus at the origin of the sciatic root of the pudic nerve; *the middle branch* is the sacral root of the pudic nerve; *the caudal branch* separates into two rami, one of which is the sacral root of the N. gluteus (N. glut.), and the other forms, with a branch from the first coccygeal nerve (q. v.) and a branch from the pudic, a slender nerve to a ribband muscle (Fig. M?) described below v. N. Coccygeus.

#### N. GLUTEUS SUPERIOR.

At the union of the lumbo-sacral cord with the first sacral nerve to form the main trunk of the great sciatic, a large branch, the superior gluteal nerve (N. gl. S.), is sent laterad and bends over the dorsal border of the ilium just cephalad of the acetabulum and entad of the MM. glutei. It leaves the pelvis by the great sciatic foramen, and 10 mm. peripherad of its origin divides into three branches; *the*



*cephalic branch* is distributed to the M. gluteus medius (M. gl. med.), which lies ectad of the nerve and whose ental surface it penetrates; *the caudal branch* is distributed to the M. gluteus minimus (M. gl. min.), which lies entad and caudad—these two rami are the homologue of the *superior branch* of anthropotomy; *the middle branch*—inferior of anthropotomy—the largest branch, perforates the M. gluteus minimus and innerves the M. tensor vaginæ femoris (T.V.F.), in which it can be traced to the distal fourth. A few filaments are given to the M. gluteus minimis.

#### N. ISCHIADICUS.

The great sciatic nerve (Fig. Ischiad.) is the largest of the spinal nerves; its ectal origin is the sacral plexus, or the union of the first and second sacral nerves. Within the pelvis, its course is caudad to the sciatic foramen; peripherad of the pelvis it lies upon the ectal border of the M. obturator internus and the MM. gemelli, mesad of the great trochanter, laterad of the ischiac tuberosity, and entad of the MM. pyriformis, biceps and glutei. Its exposure is effected in the meros by the removal of the M. gluteus maximus and the M. biceps. The great sciatic nerve is cutaneous and muscular in its distribution; it supplies the integument of nearly all the caudal limb, and the muscles of the meros, the crus, and the pes as given below.

*Principal Rami.*—*The first branch* is given off at the union of the second sacral nerve, and innerves the M. quadratus femoris (Fig. Quad.). *The second branch* is the sciatic root of the pudic nerve (q. v.), in common with the root of a gluteal nerve (b. v.). *The third branch* is a considerable nerve entad of the M. pyriformis, and which is divided into three smaller rami: (*a*) the first of which enters the ental surface of the M. biceps, 5–8 mm. peripherad of its origin (Fig. M. bi.); (*b*) the second is covered by the M. biceps, to which it gives it ramulus at its mesal (lower) border, and continues entad of the M. semi-tendinosus and a plexus of

vessels (ramuli of the profund artery and veins (?)); it lies upon the ental surface of the muscle 20-30 mm., then penetrates its substance as two terminal ramuli (Fig. M. semi-ten.); (c) the third ramus crosses the ectal surface of the vessels named, peripherad of which, or 20 mm. from its origin, it enters the M. semi-membranosus as two terminal ramuli (Fig. M. semi-mem.). *The fourth branch* is a slender filament, about the middle of the thigh, which is given to the distal half of a ribband muscle (Fig. M?) 2 mm. in width, which lies in the fascia upon the ental surface of the M. biceps, which muscle it crosses obliquely—this muscle has its origin just cephalad of the M. pyriformis upon the diapophysis of the first caudal vertebra, lies entad of the M. pyriformis and the M. biceps, and is inserted in the aponeurotic fascia of the mesal border of the biceps about midway between knee and ankle; it is readily separable from the biceps; the total length in a cat of medium size is about 90 mm.; the proximal end of the muscle is innervated by a ramulus whose roots are traceable to the third sacral, the first coccygeal and the pudic nerves. *The fifth branch* innervates the distal third of the M. biceps (M. bi.); it is given off 40 mm. peripherad of the trochanter, just centrad of the short saphenous nerve.

#### N. CUTANEUS INTERNUS.

The short saphenous nerve (Saph. br.) has its ectal origin just centrad of the division of the sciatic trunk into the popliteal and the peroneal nerves. It crosses the popliteal space embedded in the adipose which occupies this region, is ectad of the artery and entad of the M. biceps; it lies apposed to the artery upon the dorsal surface of the biceps and entad of the ectal fascia. Its filaments terminate in the integument over the caudal side of the foot and the fifth toe.

The great sciatic trunk divides into two unequal nerves, the caudal and smaller, N. peroneus, and the cephalic, larger nerve, N. popliteus.

## N. PERONEUS.

This nerve lies entad of the insertion third of the M. biceps and ectad of the M. gastrocnemius, which muscle it crosses a bout 10 mm. peripherad of the caudal condyle. As the nerve dips between the M. peroneus longus and the M. peroneus tertius, the

## N. MUSCULO-CUTANEUS

(Fig. mus.-cut.) takes its origin and has its course entad of the M. peroneus, apposed to the anterior tibial artery; it becomes ectal (superficial) with the artery about midway between the knee and the ankle, or near the tendinous part of the M. peroneus longus; following the artery its ramuli may be traced to the integument upon the dorsum of the foot and the second, third and fourth toes. Its caudal filaments anastomose with the short saphenous nerve. Ten mm. peripherad of its origin it gives a branch to the M. peroneus tertius, and 10 mm. still peripherad a large ramus passes entad and lies upon the ectal surface of the M. peroneus brevis, apposed to an arteriole (a branch of the anterior tibial artery), which muscle it innerves. The trunk crosses the ectal surface of the muscle (peroneus brevis) obliquely and bends around the caudal border of the large tendon as it passes through the sheath caudad of the malleolus; it then lies entad of the tendon and upon the ectal surface of the short extensors of the toes, which muscles it penetrates, lying between the fourth and the fifth metatarsalia, and entad of the tendon to the fifth toe, but ectad of the one to the fourth toe at the distal end of the metatarsale, at which point it joins a ramus of the (?) nerve, thence it is distributed to the integument of the fourth toe.

The nerve trunk at the origin of the musculo-cutaneous branch gives a ramus to the overlying M. peroneus longus, which nerve accompanies an arteriole from the anterior tibial artery. Entad of the M. peroneus longus with the last

described nerve, an equally large branch lies just entad and dips between the M. extensor digitorum longus and the M. peroneus tertius. Ten mm. peripherad of its origin the nerve bifurcates, the anterior tibial artery (Fig. A.) occupying the angle between the branches. *The cephalic branch* (Fig. cc.) innerves the M. extensor longus digitorum; *the caudal branch* (Fig. ca.) lies entad of the anterior tibial artery and accompanies the artery to the dorsum of the foot. Entad of the groove a ramus is given to the tarsal ligament and the origin fibres of the M. extensor brevis. The terminal filaments join in the plexus to the integument of the dorsum of the foot and toes.

#### N. TIBIALIS ANTICUS.

This branch (Fig. Tib. a., and m.) of the peroneal is given off between the origin of the musculo-cutaneous nerve and the bifurcation of the peroneal; it can be traced 30-40 mm. in the substance of the M. tibialis anticus, and sends a ramus peripherad to the M. extensor longus digitorum.

#### N. POPLITEUS.

The cephalic division of the great sciatic nerve crosses the popliteal space and continues peripherad between the heads of the M. gastrocnemius. At the proximal end of the crus it gives its *first branch* to the ectal surface of the caudal head of the M. gastrocnemius (Fig. M. gas.), and immediately peripherad a large ramus penetrates the same muscle and is distributed to the muscle from its ental surface; a considerable portion of this ramus perforates the gastrocnemius and innerves the M. Soleus (Sol.), which is entad; from this penetrating ramus ramuli are given to both heads of the muscle. Twenty mm. peripherad a *second large branch* to the body of the same muscle (Fig. M. gas.), peripherad of which the nerve trunk bifurcates, forming ental (Fig. dv. ent.) and ectal (Fig. dv. ect.) divisions.

## N. POST-TIBIALIS.

The *ental division* of the popliteal nerve is muscular in distribution. Ten mm. peripherad of its origin a large ramus innerves the M. popliteus (Fig. Pop.), which lies just entad. The trunk crosses the ectal surface of the post-tibial artery, and 10 mm. peripherad it innerves the M. flexor longus digitorum (M. fl. long. dig.) by several pinniform ramuli. As the nerve penetrates the flexor muscle a ramus is given to the M. tibialis posticus, and still peripherad three or four filaments are given to the M. flexor longus pollicis?—a muscle whose tendon unites in the plantar surface with the broad tendon of the long flexors (pollex is wanting in the cat).

The *ectal division* lies apposed to the post-tibial artery and gives no rami centrad of the groove of the long flexor muscle, in which groove are the tendon, the nerve and the post-tibial artery. Peripherad of the groove the nerve bifurcates and lies upon the ental surface of the M. flexor brevis digitorum. The cephalic ramus,

## N. INTER-PLANTARIS,

innerves the short flexor muscles, lies along its cephalic border, and terminates in cutaneous ramuli to the pads of the second and third toes; a few filaments are directed entad to the underlying muscle, the M. flexor accessorius (fl. ac.).

## N. PLANTARIS,

The caudal ramus of the ectal division, lies upon the broad tendon of the long flexor muscle and the second layer of muscles. A slender ramus is given caudad to a small muscle upon the distal end of the calcaneum—the fibres of this muscle run transverse and the aponeurosis joins the broad tendon of the long flexor. Near the proximal end of the meta tarsalia a branch is given entad,



## THE ENTAL PLANTAR NERVE,

which lies ectad of the proximal end of the interosseus muscles and within their substance, and crosses the foot obliquely from the head of the metatarsale of the fifth toe toward the distal end of the metatarsale of the second. The nerve trunk lies entad of the caudal border of the short flexor and at the distal end of the second metatarsale (pollex wanting); it divides into a leash of four nerves, each of which dichotomoses and innerves the interosseous muscles (M. int.); slender filaments are given to the third layer of muscles. The ental branch innerves the third and fourth lumbricales, the three plantar interossei muscles, and the four muscles which occupy the plantar arch of the metatarsalia—these muscles have their origins at the proximal end of the metatarsalia and insertion in the aponeurosis of the common extensor tendon and by a short tendon into the proximal end of the proximal phalange. A portion of the muscle seems to be equivalent to the dorsal interossei (anthropotomy), and a portion is not satisfactorily homologized. The deep plantar also innerves a muscle, which has its origin from the os cuboides and crosses the plantar metatarsus obliquely and inserts by a tendon upon the caudal surface of the proximal phalange of the second toe, probably an adductor muscle.

## THE ECTAL PLANTAR NERVE

bends around the tendon of the muscle, and, crossing its ectal surface, lies entad of the tendon of the long flexor of the second toe. At the distal end of the proximal segment of the fifth toe it bifurcates, and can be traced to the pad of the fourth and fifth toes. A slender filament is given to the M. abductor minimus (Fig. M. ab. min.).

## N. PUDICUS (N. PUDENDUS).

The pudic nerve (Pud.) has its ectal origin by two roots. The sacral root is the largest of the terminal branches of the

third sacral nerve, and lies entad of the pudic artery; the sciatic root is given off from the sciatic nerve about 15 mm. peripherad of the union of the first and second sacral nerves, in common with the sciatic root of the N. gluteus to the M. glutei (Fig. N. glu.). It leaves the pelvis through the sacro-sciatic foramen, and is apposed to the pudic artery; its general course is meso-caudad, entad of the pudic artery and vein, upon the ectal surface of the internal obturator muscle. Twenty mm. peripherad of the union of the two root nerves, the pudic separates into dorsal and ventral divisions, which are muscular and cutaneous respectively in distribution.

#### N. PERINEUS DORSALIS,

*The dorsal division* (Fig. dor.), lies upon the ectal surface of the rectal muscle; its branches innerve the broad M. levator ani (Fig. L. A.), the M. sphincter ani (Fig. sph. A.), and 20 mm. of the longitudinal rectal muscles (Fig. rec.), which muscles are supplied by the hemorrhoidal artery and vein. The last nerve is the

#### N. HÆMORRHOIDES.

A branch is given to the anal gland (Fig. gl.)—a large olive-colored gland just laterad of the anus, whose duct opens ectad of the sphincter muscles, or sometimes just entad. Another ramus,

#### N. PERINEUS DORSALIS,

Innerves the sphincter vaginæ and the ectal labium(?).

#### N. PERINEUS VENTRALIS,

*The ventral division* (Fig. ven.), is distributed to the vagina, the ectal labium, the perineum, the urethra, the M. accelerator urinæ, and the transverse muscle just entad of the perineal integument. A considerable ramus is given to its plate-trope (Plat.) in the meson, and the nerve terminates as a large nerve in the glans clitoridis (N. dorsalis penis seu clitoris,

Fig. Cl.), the peripheral 5 mm. being parallel with its plate-trope.

#### NN. COCCYGEI.

The coccygeal nerves are seven or more pairs, and with the exception of the first (cephalic) one, innerve the caudal muscles and integument. They decrease in size caudad, until it may be questioned whether the extreme filaments are properly designated nerves. The ectal root fibres are attenuated and the dorsal ganglion is hardly distinguishable caudad of the seventh; hence I have mentioned the number as seven. Like the other spinal nerves, they divide into dorsal and ventral divisions; *the dorsal* innerve the dorsal muscles and integument and form the roots of a single nerve trunk,

#### N. DORSALIS

(Fig. dor.?), caudad of the seventh caudal vertebra, whose filaments innerve the adjacent structures. *The ventral* divisions join their fellows to form a ventral nerve trunk,

#### N. VENTRALIS

(Fig. vent.?). The rami of the ventral trunk have a two-fold distribution; the first ramulus innerves the ental or the inter-vertebral muscle (Fig. M. ent.), and midway between the several pairs a ramulus innerves the ectal muscle of the tail (Fig. M. ect.). The plan of formation of the dorsal and the ventral caudal nerves is seen in the diagram (Fig. B).

#### N. COCCYGEUS CEPHALICUS.

The first coccygeal nerve has a distinctive distribution, and requires a separate description. The ventral division separates into a ventral and a dorsal or caudal branch. *The ventral branch* becomes the anastomotic loop to the third sacral nerve, the coccygeal or principal root of the

## N. COCCYGEUS

(Fig. N. coc.) to the muscle by the same name, one root of a nerve to the urocyst (Fig. Uro.), and one root of the nerve to the ribband muscle ? (Fig. M.?).

## RECAPITULATION.

The cat is a good type for the study of comparative anatomy. The nervous system offers special advantages, as a basis of comparison, for establishing homologies, for identification, etc.

Zoöotomy should precede anthropotomy in the collegiate and the medical curricula.

*Preparation.*—Injection of arteries and veins with *starch injection mass*.

*Posture.*—Ventre-cumbent, head sinistrad.

*Exposure.*—By reflection of integument over caudal thorax, sinistral side, beginning with removal of neural arch of caudal thoracic vertebra; dissection caudad.

## LUMBAR NERVES.

*Characters in common:* Paired; dorsal and ventral divisions at ectal origin; related with sympathetic system; muscular and cutaneous in distribution; two groups, *cephalic four* not involved in lumbar plexus, *caudal three* so involved; the cephalic group innerve muscles and integument of back, MM. psoas, phrenicus, abdominis entalis, ectalis, transversalis and rectus, and the abdominal integument.

*N. Genito-cruralis.*—*Origin:* Fifth and sixth lumbar nerves, *two roots*. *Distribution:* *Crural* division, integument of caudal meros, and proximal crus; anastomoses with N. N. cutaneus ectalis; *genital* division, plexus at ilio lumbar artery, hypogastric and ventro-perineal integument.

*N. Cutaneus Ectalis.*—*Origin:* Loop and sixth lumbar nerve, *two roots*. *Distribution:* Integument of hip and thigh, joins last described nerve.

*N. Cruræus Anterior.*—*Origin:* Seventh lumbar. *Distribution:* MM. psoas, iliacus, sartorius, vastus externus, V. internus, rectus femoris, cruræus, pectineus, and gives origin to

*N. Cutaneus Internus Longus.*—*Distribution:* To integument of cephalic crus, dorsum of foot and plantar plexus.

*N. Obturator.*—*Origin:* Loop between seventh lumbar and first sacral nerves, *lumbo-sacral cord* (anthropotomy). *Distribution:* MM. pectineus, obturator, adductor magnus and longus, gracilis.

#### SACRAL NERVES.

*Characters in common:* Paired, three pairs; dorsal and ventral divisions; related with sympathetic system; muscular and cutaneous; unequal size; formation of sacral plexus, which is the origin of several nerves.

*Special Characters:* *First sacral nerve*, largest of spinal nerves; joined with the lumbar cord in the lumbo-sacral cord.

*N. Gemellus.*—*Origin:* Ramus of first sacral at foramen of exit. *Distribution:* M. gemellus superior.

*Second Sacral Nerve.*—Much smaller than the first nerve; union with first nerve forms N. ischiadicus; joins the third nerve in the anastomotic loop.

*Third Sacral Nerve.*—Smallest sacral nerve; joins sacral and coccygeal plexuses; innerves the M. levator ani; the urocyst; by its rami becomes the sacral root of NN. coccygeus, gluteus, pudicus, and a nerve not homologized.

*N. Gluteus Superior.*—*Origin:* Sacral plexus at first sacral nerve. *Distribution:* Cephalic branch to M. gluteus medius, caudal branch to M. gluteus minimus, middle branch to M. tensor vaginæ femoris.

*N. Ischiadicus.*—*Origin:* Union of first and second sacral nerves. *Distribution:* MM. quadratus femoris, glutei, pyramiformis, biceps, semi-tendinosus, semi-membranosus, obturator internus, ribband muscle?.



*Rami Known as Nerve Trunks.*—NN. pudicus, cutaneus internus brevis, popliteus, peroneus, gluteus, q. v.

*N. Peroneus.*—*Origin:* Division of N. ischiadicus centrad of knee. *Distribution:* *Rami:* *N. musculo-cutaneus*, integument of dorsum of foot, and second, third and fourth toes, M. peroneus brevis, M. peroneus tertius; *N. tibialis anticus*, MM. tibialis anticus, extensor longus digitorum, extensor brevis digitorum; ligamentum tarsale; plexus dorsalis pedis.

*N. Popliteus.*—*Origin:* Division of N. ischiadicus, centrad of knee. *Distribution:* MM. gastrocnemius, soleus, popliteus, flexor longus digitorum, tibialis posticus, flexor longus pollicis(?), flexor brevis digitorum, transversus, abductor minimi, interossei; integument of foot and pads.

*N. Pudicus.*—*Origin:* Two roots, sciatic and sacral. *Distribution:* *Dorsal* division, to MM. levator ani, sphincter ani; rectum, vagina, anal gland; *ventral* division, to M. accelerator urinæ, perineum, vagina, ectal labium, urethra, glans clitoris, platetropæ.

#### COCCYGEAL NERVES.

*Characters in common:* Paired, seven or more pairs; great length of ectal roots; rapid decrease in size, caudad; dorsal and ventral divisions; dorsal divisions unite to form a dorsal trunk, N. dorsalis, and the ventral divisions form ventral trunk, N. ventralis.

*Distribution:* Muscles and integument of tail.

*N. Coccygeus cephalicus.*—*Origin:* First coccygeal nerve. *Distribution:* MM. levator ani, sphincter ani; gives anastomotic loop to third sacral nerve in the sacral plexus; by its rami forms the coccygeal roots of several nerves—N. coccygeus, nerve to the urocyst, nerve to ribband muscle.

#### DESCRIPTION OF DIAGRAM.

*A. fem.*, arteria femoralis; *Acc.*, musculus accelerator urinæ; *anas.*, N. anastomoticus; *Ca.*, divisio caudalis; *Ce.*, divisio cephalica; *Cl.*, glans clitoris; *crur.*, crural division of the genito-crural nerve; *dac.*,

dactylus; *Dia.*, diaphragm; *M. phrenicus*; *Dv. dor.*, divisio dorsalis; *Dv. ven.*, divisio ventralis; *Em.*, foramen exitus; *gen.*, genital division of the genito-crural nerve; *Gl.*, glandula ani; *H.*, hip, integument over the gluteal region; *int.*, integument, cutaneous nerve; *isch.*, ischium; *k.*, knee; *Lab.*, labium ectale; *loop*, anastomotic nerve joining nerve trunks in plexiform relation; *L.-S. C.*, lumbo-sacral cord; *l.r.*, ramus lateralis; *M.?*, muscle not identified, v. text; *M. ad. long.*, *M. adductor longus*; *M. ad. mag.*, *M. adductor magnus*; *M. bi.*, *M. biceps*; *M. crur.*, *M. cruræus*; *M. dor.*, *musculi dorsales*, quadratus lumborum, erector spinæ, inter-vertebrales, etc.; *M. ect.*, *M. obliquus abdominis ectalis*; *M. ent.*, *M. obl. abd. entalis*; *M. flex. long. dig.*, *M. flexor longus digitorum*; *M. flex. br. dig.*, *M. flexor brevis*; *M. flex. long. pol.*, *M. flexor longus pollicis*; *M. gas.*, *M. gastrocnemius*; *M. gl. max.*, *M. gluteus maximus*; *M. gl. med.*, *M. medius*; *M. gl. min.*, *M. minimus*; *M. gl. S.*, *M. superior*; *M. grac.*, *M. gracilis*; *M. ili.*, *M. iliacus*; *M. l. A.*, *M. levator ani*; *M. obt.*, *M. obturator*; *M. obt. int.*, *M. internus*; *M. pec.*, *M. pectineus*; *M. pso.*, *M. psoas*; *M. pyr.*, *M. pyriformis*; *M. quad.*, *M. quadratus femoris*; *m.r.*, ramus mesalis; *M. rect.*, *M. abdominis rectus*; *M. fem.*, *M. rectus femoris*; *M. sar.*, *M. sartorius*; *M. semi-mem.*, *M. semi-membranosus*; *M. semi-ten.*, *M. semi-tendinosus*; *M. sph. a.*, *M. sphincter ani*; *M. tib. p.*, *M. tibialis posticus*; *M. trans.*, *M. abdominis transversalis*; *M. T. V. F.*, *M. tensor vaginæ femoris*; *M. v. ext.*, *M. vastus externus*; *M. v. int.*, *M. vastus internus*; *N. coc.*, *N. coccygeus*; *N. crur.*, *N. ramus cruræus*; *N. gem.*, *N. gemellus*; *N. gen.*, *N. ramus genitalis*; *N. glut.*, *N. gluteus*; *N. gl. s.*, *N. gluteus superior*; *N. mus.-cut.*, *N. musculo-cutaneus*; *N. obt.*, *N. obturator*; *N. per.*, *N. peroneus*; *N. pop.*, *N. popliteus*; *N. saph. br.*, *N. cutaneus internus brevis*, short saphenous; *N. saph. l.*, *N. cutaneus internus longus*, long saphenous; *P.* Poupart's ligament; *peri.*, perineum; *plat.*, platetropé; *Pl. plan.*, Plexus plantaris; *Pl. S.*, plexus solaris; *pub.*, pubes; *S.*, ganglion sympathicum; *Th.*, integument over the meros, thigh; *ure.*, urethra; *uro.*, urocystis; *vag.*, vagina.

## WEIGERT'S METHOD OF STAINING THE MEDULLARY SHEATH OF NERVES.(<sup>2</sup>)

In the paper quoted, Dr. Weigert gives a full account of the famous method bearing his name, together with a historical review of the stages in its differentiation.

The method, as now revised, consists of four stages, as follows: (1) Hardening in chromic salts; (2) introduction

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<sup>1</sup> WEIGERT, "Zur Markscheidenfärbung" Deutsche medicinische Wochenschrift. Festnummer zur Ehren Rudolf Virchows, October 13, 1891.

of copper in the chromium compound within the sheaths; (3) staining with hæmatoxylin; (4) differentiation by means of borax-ferricyanid of potassium. The precipitate which tends to appear during the staining is prevented by the addition of the carbonate of lithium.

The modified method, as here published for the first time, is as follows: Fragments suitable for microscopic sections are thoroughly hardened in bichromate of potassium, and, after treatment with alcohol, are imbedded in celloidin. After coagulation in 80 per cent. alcohol they were, according to the old method, brought into a solution of neutral cupric acetate in an equal volume of water and kept in the brood-oven twenty-four hours. The modification consists in the substitution of equal volumes of neutral cupric acetate and tartrate of soda ( $C^4H^4O^6KNa+4H^2O$ ). Large fragments may remain for forty-eight hours without injury, provided the temperature is not permitted to rise too high. The fragment then is passed into an aqueous solution of cupric acetate and remains twenty-four hours longer in the warm chamber. After rinsing, the specimens go into 80 per cent. alcohol, where they become available for sectioning any time after an hour or so.

For staining, two stock solutions are required: (*A*) 7 c.cm. saturated aqueous solution of carbonate of lithium + 93 c.cm. distilled water; (*B*) 1 gm. hæmatoxylin + 10 c.cm. alcohol. These are to be combined just before using in the proportion of 9 volumes of *A* to 1 volume of *B*. Sections stain in three or four hours, though the staining is not injured by leaving them twenty-four hours in the fluid. This process is, unfortunately, only available for free sections, which then require no development, but, after rinsing, are brought into 90 per cent. alcohol and are cleared in a mixture of 2 volumes of analin oil + 1 volume of xylol, followed by pure xylol and balsam.

## THE DEVELOPMENT OF THE CRANIAL NERVES OF VERTEBRATES.<sup>(1)</sup>

PROF. C. VON KUPFFER.

Tracing their origin, these cells are seen to proceed from the epidermis. The latter thickens by elongation of its elements, which then divide transversely, after which the ental layer of daughter cells do not reassume their epithelial arrangement, but constitute the special sub-epidermal layer or neurodermis. The latter has in any case a close relation with the development of the peripheral part of the branchial nervous system, evidence of which is furnished by the fact that the thickening of the epidermis, which precedes the development of this structure, is derived from the rudiment of the epibranchial ganglion.

It is cells of this layer which furnish the first commissures connecting the epibranchial ganglia with each other, as well as with the preformed branchial nerves and with the definitive (principal) ganglia. It may, therefore, be said that the epidermis contributes to the development of the peripheral branches of the branchial system, but whether these cells play a rôle in the formation of the fibrillæ, or simply have a secondary significance, cannot be determined at present.

### CRANIAL NERVES OF YOUNG AMMOCETES.

After this exposition of the main features in the develop-

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Translated for this journal, from advance sheets, by OLIVER S. STRONG, Fellow in Biology in Columbia College.

ment of the cranial nerves, I pass on to their description in young *Ammocætes*, which, when fixed (sublimate, alcohol), measure  $3\frac{1}{2}$ – $3\frac{3}{4}$  mm. While living they might have been fully 4 mm. The stage of development of these specimens, upon which I base my description, is as follows: There are seven pairs of gill pouches present; the hindmost (eighth) pair is in formation. In the foremost, obliquely placed and temporary pair of pouches, the withdrawal of the endoderm from the epidermis has already taken place and the mesoderm interposed. The diaphragms in the pouches are not yet formed; outer spiracles are still wanting throughout. The septum between the oral cavity and the branchial gut is not yet perforated, but is thinned, and the formation of the stomodæum from pouches, described by Dohrn,<sup>(1)</sup> whereby the free surface of the velum is enlarged, has set in. There is as yet no pigment in the eye, the lens is constricted off, and the recessus labyrinthi extends dorsad to the exit of the roots of the facial. There exist three pronephric canals with funnels formed, and on each side a large glomerulus. The pronephric duct reaches the hind gut.

#### BRANCHIAL SYSTEM.

I begin with the description of the branchial system of the cranial nerves of this larva, referring to Fig. 8, which is drawn from three sagittal series of sections, and shows the roots, ganglia and peripheral nerves of the system projected on the median plane. One sees in the figure two rows of ganglia, *i.e.*, dorsally the row of large or principal (*Hauptganglion*) ganglia (I–V), and ventrally, over the gill septa (gill arches), the epibranchial ganglia (1–12) bound by commissures into one cord. A third row of ganglia is shown in the drawing between the gill pouches.

1. *Region of the Trigeminus*.—The two principal ganglia of this region are plainly set off from each other. The first

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1 DOHRN, XII, "Studies," 1888, p. 238–239.



is somewhat smaller than the second, and has an approximately triangular shape, the base directed dorsad. It lies over the eye. From the fore corner there go out two stout nerve trunks, which proceed in an arch cephalad and ventrad. In the ganglion two portions may be distinguished. The dorsal, broader part is traversed by fibrillæ which proceed, in direction, from the roots to the branches; in the ventral, tapering part no fibrillæ can be perceived among the nerve cells.

The second principal ganglion, more voluminous than the first, has also a stouter root (perhaps already two). It lies over the stomodæum and likewise displays two divisions, which have the same relations as those of the first principal ganglion; fibrillæ traverse the fore dorsal part, the hinder part appear free of fibrillæ. From the fore part there go close together the two branchial nerves, the N. maxillaris and N. mandibularis. Both consist of a compact cord of fibres, which contains nuclei within, and at the surface shows an envelope of cells.

The epibranchial ganglia of this region show a continuous chain which impinges cephalad upon the lens, *so that it appears as the foremost part of the chain*. One can distinguish between the lens (it not being reckoned in) and the N. mandibularis, three parts of the chain, marked off by constrictions, which may be designated the first, second and third epibranchial ganglia. The first is inserted slightly under the lens, the second projects somewhat dorsally and is directly connected with the first principal ganglion. The third epibranchial ganglion lies at the lateral side of the origin of the NN. maxillaris and mandibularis, and stands in broad connection with the cell mass of the second principal ganglion.

2. *Region of the Acustico-Facialis*.—The facial ganglion and the auditory vesicle of the principal ganglia belong to the series. The principal ganglion of the facial projects far forward over the auditory vesicle, and its fore end lies under

the hinder surface of the second principal ganglion of the trigeminus. It reaches around the auditory vesicle on the median and ventral sides as far as its middle, and here ends in a point. The contact with the wall of the auditory vesicle is very close.

I assign to the same region two ganglia of the epibranchial chain, namely, those lying in front of the first and second gill pouches, and which, numbered from before, would be four and five. The fifth epibranchial ganglion is immediately connected with the principal ganglion of the facial, and participates in the composition of the N. branchialis, a massive cord proceeding chiefly from the principal ganglion into the hyoid arch. The diminished fore end of the principal ganglion extends into the commissure which connects the fifth with the fourth epibranchial ganglion. At this stage a short nerve "anlage" proceeds from the latter, which is produced into the substance of the mandibular arch, superficially, in a ventral direction. But this fourth epibranchial ganglion occupies an intermediate position, and is connected both with the principal ganglion of the facial and the second principal ganglion of the trigeminus. While I assign it provisionally to the facial region, this view needs to be proved by further investigations as to its later fate.

I have, from earlier stages, represented as acusticus the hinder portion of the one continuous branchial root of this region,<sup>(1)</sup> which is connected with the wall of the auditory vesicle at the base of the recessus labyrinthi, and has, at that time, developed no ganglion. It has not essentially changed from there on to the stage now under consideration. The acusticus, too, only shows here this one place of connection with the auditory vesicle. Although cells may be seen between its fibrillæ and in connection with them, they cannot yet be called a ganglion.

3. *Region of the Vagus Group.*—As belonging to this

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1 Arch. f. Mikr. Anat., 1890, Bd. 35, p. 543.

region I have described, from the stage of development reached in the days immediately preceding the exit of the embryo:<sup>(1)</sup> (1) A large isolated lateral ganglion arising from the epidermis, and located over the second and third gill pouches; (2) a medial ganglion proceeding from the root-border (*Wurzel Leiste*) and uniting with the latter; thus there are, according to my present terminology, the components of a principal ganglion of the vagus; (3) epibranchial ganglia over the second and the following gill pouches. A *lateral* ganglion assigned to the glosso-pharyngeus is developed between the auditory vesicle and the vagus, and not *isolated* from the epidermis. I supposed, therefore, that the glosso-pharyngeal ganglion described by Scott and Shipley is an epibranchial ganglion.<sup>(2)</sup> At the same time I pointed out that there is no sharp division between the facial group and that of the vagus at this stage. The epibranchial ganglion lying over the second gill pouch received a very noticeable addition from the root-border, consisting of cells and fibrillæ, but at the same time a nerve originating from the facial root sinks into this ganglion, which I called the *ramus recurrens* of the facial.

In *Ammocætes* of 4 mm. the relations are much clearer, the individual parts are more separated, and at the same time there has taken place a displacement laterad which renders easier the comparison with the relations in older *Ammocætes*. The epibranchial ganglia experience a transference caudad, so that they are no longer located over the gill pouches, but are over the corresponding gill septa (visceral arches), *i.e.*, the ganglion formed over the second gill pouch now lies directly over the septum between the second and third gill pouches. The auditory vesicle in larvæ of 4 mm. is situated over the second gill pouch, projecting somewhat beyond it both caudad and cephalad. As the principal ganglion of the facial lies close to the wall in the fore half of the auditory

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<sup>1</sup> *Ibidem*, p. 544.

<sup>2</sup> *Ibidem*, p. 552.

vesicle, so is the ganglion of the glosso-pharyngeus in close contact with its caudo-ventral wall, and has fused with the portion of its cells which I have mentioned and drawn as the sickle-shaped investment of this part of the wall of the vesicle.<sup>(1)</sup> This cell-girdle, up to the time of the exit of the embryo is continuous with the mass of the principal ganglion of the facial, and I have accordingly assigned it to the latter. But it changes later. In larvæ of 4 mm. the separation is completed, and the cell group under consideration has by this time connected itself with the glosso-pharyngeus. It thus comes to pass that the continuous cell mass, which originates from the epidermis in closest contact with the labyrinth pit and is further augmented by the cells of the wall of the latter, embraces the lateral portions of two ganglia, the larger fore part going over to the principal ganglion of the facial and the smaller hind part to the ganglion of the glosso-pharyngeus. Along with this the glosso-pharyngeus moves out of the particular place which I believe must be assigned to it originally, before the separation of the ganglion mass adjoining the labyrinth vesicle into two parts has been completed.

As the glosso-pharyngeus is now, it consists of a stout fibrillar root, which is evidently separated from the acusticus but unites with the vagus root lying caudad. The root enters an elongated ganglion whose medial part, likewise present from the first, has united secondarily with the lateral part which was joined to the labyrinth vesicle. This principal ganglion, extending further, now fuses with the epibranchial cord, so that it completely takes in the sixth epibranchial ganglion. At the same time, however, it connects itself, by a tract (Zug) directed cephalad, with the fifth epibranchial ganglion. The latter is thereby closely related both to the facialis and to the glosso-pharyngeus.

The relations of the vagus, in the strict sense, when

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1 Arch. f. Mikr. Anat., 1890, p. 524, Figs. 54, 74.

compared with the earlier stages, have changed the least.

Its large principal ganglion, arising typically, lies above the septum between the third and fourth gill pouches and over the fourth pouch itself. The short, stout, single root is mostly fibrillar, but also contains cells, both in the interior and as an envelope outside. It sinks into the cephalo-dorsal angle of the ganglion. The hind point of the approximately triangular ganglion extends into the N. lateralis, entirely lacking ganglia, which ends in the caudal half of the trunk in a swelling of the epidermis. The cephalo-ventral angle of the principal ganglion sends out the stout N. branchio-gastricus, rich in cells, which connects itself with the seventh epibranchial ganglion (numbering from before). Five more ganglia lie behind this in the epibranchial cord. There are thus found in the whole chain, which extends from the eye to behind the eight gill pouches, altogether *twelve epibranchial ganglia*.

#### THE BRANCHIAL NERVES.

I begin with those lying caudad, where the relations are simplest. The *hindmost* five branchial nerves have the same relations. Each one arises as a cord from the appropriate epibranchial ganglion, and is connected by means of a second more slender cord with a sympathetic ganglion of the spinal system. It proceeds then ventrally into the gill arch and divides into a cutaneous and a muscular branch. The cutaneous branch is the foremost, and connects itself with a rounded protuberance of the epidermis projecting ventrad. The muscular branch accompanies the arch of the aorta ventrad and ramifies further (Fig. 9). The external spiracula (gill openings), which are formed behind the pertaining gill pouch, have arisen. Thus the cutaneous branches are shown to be the rami prætrematici, and the epidermal prominences small separated ganglia, which I will denote as ganglia prætrematici.



The sixth branchial nerve, numbered from behind, arises from that epibranchial ganglion which the N. branchio-gastricus of the vagus enters. Here, as well as with the branchial nerves lying cephalad, it can be established that their most important part is derived from the principal ganglion, and that the portions derived from the epibranchial and sympathetic ganglia are the smaller.

The branchial nerve of the glosso-pharyngeus, the seventh from behind, and that of the facialis behave like the foremost one of the vagus. All these nerves divide within the gill arch into the cutaneous and muscular branches, the first of which fuses with an epidermal prominence, the subsequent ganglion prærematicum.

In the region of the four anterior epibranchial ganglia this arrangement is destroyed, owing to the stomodæum, and the interpretation of the peripheral nerves present here is difficult. Three nerves come into consideration, namely: (1) A short nerve springing from the fourth epibranchial ganglion (numbered from before), which proceeds behind the N. mandibularis to the epidermis and ends in a small ganglion (probably the r. mand. ext., Fürbringer); (2) the N. mandibularis, which, as a stout fibrillar cord, leaves the second principal ganglion of the trigeminus and derives the greater part of the fibrillæ directly from the branchial root; a more slender cord from the third epibranchial ganglion joins this; (3) the N. maxillaris; this arises from the principal ganglion and the second epibranchial ganglion. I must let it remain undetermined whether the first epibranchial likewise has a share in this nerve. The N. maxillaris divides into branches for muscles in the upper lip, for the side wall of the stomodæum and for the skin of the lip. A twig proceeding along the skin ends in a ganglion lying close under the epidermis, which behaves entirely like the prærematic ganglia of the gill region.

There are thus always present in the region of the trigeminus small ganglia of a third series, which I might annex

to the prærematics of the gill region, and it is worth noticing that such a one lies in front of the stomodæum.

Since at least one epibranchial ganglion participates in the formation of the N. mandibularis, as well as of the N. maxillaris, I regard both nerves as homodynamous to at least one branchial nerve, but reserve a final judgment as to their value.

I cannot clearly demonstrate a participation of the first epibranchial ganglion, impinging upon the lens, in the formation of peripheral nerves.

#### SPINAL SYSTEM OF CRANIAL NERVES.

The determination of the parts of this system encounters great difficulties. The somites, which are present only a short time between the ear and eye, already dwindle away a perceptible time before the exit of the embryo, and with them the dorsal branches of the dorsal spinal nerves. The principal ganglia of the branchial system, the eye and the lateral muscles of the head growing cephalad take up so much space that the spinal nerves have to be sought in narrow interspaces. In every case they are less developed than those of the branchial system. One does not meet compact cords in the developmental stage under consideration, but only loose strands of fibrillæ connected with cells. One applies himself with more advantage to the ganglia than to the roots for the determination of their number and arrangement.

One encounters the foremost ventral spinal nerve, the root and the little ganglion of a dorsal spinal nerve, which I regard the foremost almost in a single transection (Fig. 10, *vs*, *ds*). This spinal ganglion lies between the secondary optic vesicle and the brain. In a cross section close behind this there lies a second ganglion, ventrad from the first, on the outer wall of a blind extension of the aorta. It is connected with the first, and I can regard it only as the foremost sympathetic ganglion.

The foremost ventral spinal nerve is a short fibrillar cord, with cells disposed in and on it, which springs from the ventral aspect of the mid-brain close outwards from its basal plate. It proceeds between the fore end of the chorda and the aorta, and approaches a hollow epithelial cord which serves to connect with each other, under the end of the chorda, a pair of bodies rich in yolk and lying laterally. There can be not doubt but that these two bodies are the head cavities which Dohrn<sup>(1)</sup> describes and from which he derives the eye-muscles. If, however, Dohrn made his observation upon these, the median piece connecting them would not be a ventral but a dorsal structure, because the carotis lies beneath it; so I must call attention to the fact that this connecting part has its location over the carotis, indeed, but under the blind foremost terminal piece of the aorta. Recently Dohrn, departing from his earlier view, states that the middle connecting part originates, in fact, from the median fusion of two entirely distinct myotomes;<sup>(2)</sup> with which I cannot agree. I consider the two head cavities under discussion, together with the cord uniting them, the foremost part of the anterior endodermal pouch which in this stage of development has even separated from the hind part of the pouch.

Peculiar as is the behavior of the nerve now in approaching this connecting piece destined to atrophy, I nevertheless believe it may be considered as the oculomotorius, since the paired præchordal head cavities, made single by the connecting piece, always participate in the formation of the eye-muscles.

I must for the present leave undetermined whether a cord which springs dorsally from the mid-brain, between the roots of the first and second principal ganglia of the trigeminus, and behind the eye approaches the second epibranchial gan-

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1 XII Studie. Mitteil. aus d. Zool. Station zu Neapel, Bd. VIII, 1887, pp. 325, 328, 330.

2 XV Studie. Mitteil. aus d. Zool. Station zu Neapel, Bd. IX, p. 332, Anmerk.

gion, persists as an eye-muscle nerve (comp. Fig. 8). Should this conjecture be established, this nerve would not belong to the spinal but to the branchial system.

If one can say that the foremost pair of dorsal and ventral spinal nerves are situated within the vicinity of the first principal ganglion of the trigeminus, in the same way one meets a second pair of dorsal spinal ganglia, connected with its sympathetic ganglia, mesad from the second principal ganglion of the same region and in the same transverse plane with the exit of the N. mandibularis from the principal ganglion just mentioned. I can state nothing definite concerning the terminal twigs belonging to this pair.

The same difficulty in following out the spinal nerves exists in the region of the facialis. The large principal ganglion and the labyrinth vesicle take up the space between the epidermis and brain almost entirely, and push the remaining elements apart. I have not been able to demonstrate a dorsal spinal nerve in the whole course, in a 4 mm. larvæ, but have, indeed, a spinal ganglion, wedged in between the principal ganglion of the facialis and the chorda, and also a long sympathetic ganglion, lying close to the aorta, which gives off fibres to the branchial nerve of the facialis. This spinal ganglion probably fuses later with the principal ganglion.

The pointed fore end of the first myomere of the body pushes up close to the hind end of the principal ganglion of the facialis, and even inserts itself slightly under the ganglion. The lateral muscles of the head do not first proceed from this, but from the second myomere, close behind the first branchial nerve of the vagus. Here, over the fore end of the second myomere, for the time being, the regular series of the spinal ganglia and spinal nerves of the trunk also begins.

This first myomere of the 4 mm. *Ammocætes* lies thus in the region of the glosso-pharyngeus, with its fore end over the second gill pouch. I have not found a ventral spinal nerve connected with the myomere, but have found a dorsal

spinal nerve with a slight ganglion, and observed its dorsal branch approach the dorsal border of the myomere and its ventral branch proceed on to uniformly small sympathetic ganglion. I do not know whether this myomere persists. But in any case the pertaining spinal nerve would not be reckoned among the cranial nerves.

I have only succeeded in demonstrating three pairs of dorsal and one pair of ventral spinal nerves of the head, and that over an extent to which belong five pairs of epibranchial ganglia.

The spinal system is therefore in *Ammocœtes*, at least in the stages of development known to me, of little value for the determination of the segmentation of the head. The epibranchial ganglia furnish the surest basis for this.

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I have enlarged so particularly on the cranial nerves of *Ammocœtes* because, on the basis of what has been communicated, I am of the opinion that here very primitive relations exist, which furnish important hints for the criticism of the cranial nerves of *Gnathostomata*. Three-fold phenomena determine me to this view: First, the far-extending formation of the epibranchial ganglia in the trigeminus region; then the close proximity of the *lens to this chain of ganglia*, whereby a new light falls upon the phylogeny of the eye; and, finally, the very important—probably preponderating—part which the epidermis plays in the formation of the principal ganglia. *As the auditory organ is referred to the series of principal ganglia, the eye appears to belong to the epibranchial series.*

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The works, already cursorily mentioned, of Van Wihje, Froriep and Beard furnish guaranty that the developmental processes, which I have described in *Ammocœtes*, also essentially recur in *Gnathostomata*. These named have not seen the separation of the first cranial nerve rudiment (*Anlage*) into spinal and branchial nerves, cephalad of the



vagus, but the formation of epibranchial ganglia from elasmobranchs on to mammalia is clearly established through their works. There remains on this side the evidence that the epidermis also participates in the principal ganglia.

There cannot be the least doubt but that the fusions, described by Van Wihje, of the ventral twigs of the facialis, glosso-pharyngeus and vagus with thickened places in the epidermis on the upper hinder wall of the pertaining gill clefts correspond to the places of formation of the epibranchial ganglia. Besides the local relations to the gill clefts or pouches, the circumstance that these places are described as starting points for the branchial terminal twigs: the rami post- and prærematici also argue for this. In sagittal sections these terminal twigs appear, in fact, as outgrowths of these ganglia, while cross sections teach that the epibranchial ganglia have, indeed, an essential but not exclusive share in the formation of the NN. branchiales.

For a time I was of the opinion that the more dorsally situated places of fusion of the dorsal branches of the cranial nerves with the epidermis, which Van Wihje mentioned, could be brought into connection with the formation of the principal ganglia. But on closer examination of the relations, this conjecture proves untenable. These dorsal branches in Selachians are purely cutaneous sensory nerves; the thickened patches of epidermis furnish the lateral organs, remaining in connection with the epidermis, and their peripheral nerve apparatus. On the other hand, the lateral portions of the principal ganglia have nothing to do, directly, with the sense organs; they separate cleanly from the epidermis, which shows thereupon a marked thinning, and move deeper within.

Beard has occupied himself more particularly than Van Wihje with these epidermal formations; only it is difficult to get a clear idea of the particulars from his publications, since this active investigator is so filled with his hypothesis of the branchial sense organs that his exposition of the de-

velopment of the cranial nerves aims before all to bring its processes into harmony with this hypothesis.

From no place in his numerous writings does it clearly emerge that he has, in general, seen or noticed the formation of the lateral portion of the principal ganglia from the epidermis. In one place<sup>(1)</sup> in his last large publication but one he says, much more explicitly, that the nerves growing out from the border (*Leiste*) connected themselves at the level of the chorda with the epidermis, which statement points to the epibranchial and not to the principal ganglia. Then, it is said further on, the dorsal branches or supra-branchial nerves arose at the *same time with the præbranchial nerves*, along with the separation from the epidermis of the ganglia that arose in the region pointed out—that is, *after* the origin of the epibranchial ganglia. This expression, also, does not permit us to suppose the formation of the dorsal branches connected with the principal ganglia, since the latter arise noticeably earlier than the epibranchial ganglia.

Also in the last treatise of Beard's, furnished with numerous figures, it is said, in accordance with the above-mentioned expression, that the cranial ganglia corresponding to the spinal ganglia received additional form-elements from the lateral epiblast *over the gill clefts and at the height of the chorda*. To draw a conclusion from this, Beard might not have seen the formation of the lateral portions of the principal ganglia, and the lateral ganglia in his and in my sense would not be identical, but Beard's lateral ganglia would correspond to my epibranchial ganglia. Nevertheless, some of his figures show that in the elasmobranchs also the epidermis forms ganglia in two well-distinguished series lying apart one over the other, lateral and epibranchial. I refer thereupon to the *Quart. Jour. Mic. Sc.*, Vol. XXVI, 1886, Plate IX, Figs. 20 and 22, on the facialis of *Torpedo*. Probably the principal and epibranchial ganglia mingle very early

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1 *Quart. Jour. Mic. Sc.*, Vol. XXVI, 1886, p. 101.

in Torpedo, whereby the perception of their separate origin is rendered difficult. This being the case, Beard's lateral ganglia would correspond to the lateral and epibranchial ganglia together in my sense. A renewed investigation of the development of the cranial nerves of elasmobranchs is necessary to obtain clearness here.

Froriep's communications are much more intelligible. In the youngest cow embryos on which he began his investigations, the principal ganglia were already formed and removed from the epidermis, so only the formation of the epibranchial ganglia could be treated of, the rudiments (*Anlage*) of which exist in Froriep's "gill cleft organs." The thickened patches of epidermis behind the eye in young cow embryos, mentioned by him, I might pronounce without hesitation to be the rudiments of the foremost epibranchial ganglia.

So that I could express from personal inspection an opinion upon the mode of formation of the cranial nerves in Amniota, I have commenced a piece of work in the Institute of this place upon bird embryos, which, begun not long ago, already has led to the result that there exists essentially a *complete agreement with the processes in Cyclostomes*. The duck appears to furnish an especially suitable object. It has become apparent that the rudiments of the cranial nerves proceeding from the root-border (*Wurzelleiste*) divide into the spinal and branchial nerves, and that these branchial nerve rudiments, while they are yet mainly composed of cells, grow distally between epidermis and protovertebræ, and on the one hand fuse with the epidermis for the formation of the principal ganglia, on the other hand, after the separation of the principal ganglia from the epidermis, enter into a second connection with it over the gill pouches.

This work has not progressed far enough to enable me to go into particulars, but this much may be said, that in the trigeminus region also the typical mode of development is preserved, since in the formation of the first principal gan-

gion of the trigeminus in the duck there can be demonstrated a very considerable participation of the epidermis. In the chick with nine to ten protovertebræ, we see the root-borders reach the dorsal border of the mesoderm. Duck embryos with eleven to twelve protovertebræ show the ganglion of the trigeminus in connection with a lateral swelling of the epidermis. Somewhat later the connection with the epibranchial ganglion appears. In the daw with twelve protovertebræ I saw a branchial nerve connected with the epidermis in both places at the same time.

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You will grant that it would be altogether premature for me to express an opinion now, more or less probable, upon the changes which the scheme of the nerves of the head of vertebrates here presented experiences up to the completion of development. The reductions, fusions, solutions of continuity and secondary connections appear to vary according to the class in very many ways.

A comparison of the representation of the branchial nervous system in the *Ammocætes* (Fig. 8) of 4 mm. with a diagram of the cranial nerves of the adult (Fig. 11) shows you how important these changes may be. I have constructed this diagram after Ahlborn's and Julin's drawings, taking into consideration also the statements of Max Fürbringer and Wiedersheim. To present a better general view, the oculomotor nerves and hypoglossus are omitted.

The whole anterior portion of the epibranchial cord, cephalad of the vagus, appears to have appeared, but is still represented by the ramus recurrens and ramus anterior of the facialis. The latter, behind and under the eye, possesses the spindle-shaped ganglion discovered by M. Fürbringer. I conjecture this ganglion to be the remnant of the foremost epibranchial ganglion or a complex of such ganglia. One might express it in this way: That in the course of development the facialis annexes all those portions of the epibranchial cord lying cephalad of the vagus. Whether the



commissure, described by Ahlborn, between the first trigeminus ganglion (Gn. ophthalmicum) and the facialis ganglion (v. Fig. 11) has also been derived from the epibranchial cord, and the latter has consequently divided as it proceeds cephalad, cannot be finally answered now, with probability, either way. But I must call attention to the fact that I did not see direct commissures between the principal ganglia, so that there is a certain warrant, pending further disclosures, in deriving all commissures in general between the vagus and trigeminus regions from the epibranchial cord.

#### DESCRIPTION OF PLATE XXII.

*Fig. 1.* *h*, neural cord; *z*, 'twixt cord (Zwischenstrang).  $\frac{6}{1}^0$ .

*Fig. 2.* *h*, neural cord; *d P*, dorsal brain-plate.  $\frac{10}{1}^0$ .

*Fig. 3.* *h*, fore brain; *a*, rudiment of eye; *d P*, dorsal brain-plate; *n*, rudiment of nerve; *g*, ganglion.  $\frac{20}{0}^0$ .

*Fig. 4.* *h*, mid brain; *l*, root-border; *m*, mesoderm; *ch*, chorda, *d*, gut; *gl*, lateral ganglion. *ge*, epibranchial ganglion.  $\frac{20}{1}^0$ .

*Fig. 5.* *h*, mid brain; *ch*, chorda; *d*, gut; *m*, mesoderm; *l*, root-border; *ns*, dorsal spinal nerve; *nb*, branchial nerve; *gl*, lateral ganglion; *gm*, medial ganglion.

*Fig. 6.* *h*, hind brain; *l*, root border; *ns*, dorsal spinal nerve; *nb*, branchial nerve; *gl*, lateral ganglion of vagus; *ge*, epibranchial ganglion; *gs*, sympathetic ganglion; *nd*, neurodermis.  $\frac{20}{1}^0$ .

*Fig. 6.* *h*, hind brain; *ch*, chorda; *d*, gut; *m*, mesoderm; *ns*, dorsal spinal nerve; *nb*, branchial spinal nerve; *gl*, hind end of lateral ganglion of vagus; *ge*, epibranchial ganglion; *nd*, neurodermis.

*Fig. 7.* *h*, fore brain; *gm*, medial ganglion; *gl*, lateral ganglion, both belonging to the I principal ganglion of the trigeminus; *ge*, epibranchial ganglion; *ns*, dorsal spinal nerve; *nd*, neurodermis.  $\frac{10}{1}^0$ .

*Fig. 8.* Branchial nervous system of an *Ammocetes* 4 mm. long, projected on the median plane, about  $\frac{10}{1}^0$ . *A*, eye; *N*, nose; *O*, ear; *I*, first, *II*, second principal ganglion of the trigeminus; *III*, principal ganglion of facial; *IV*, principal ganglion of glosso-pharyngeus, fusing ventrally with the sixth epibranchial ganglion; *V*, principal ganglion of vagus, first, seventh and twelfth epibranchial ganglia; *K*<sup>1</sup>-*K*<sup>8</sup>, gill pouches; *ch*, chorda; *l*, nervus lateralis. Going out from the epibranchial ganglia and proceeding ventrally between the gill pouches are the terminal branches of the branchial nerves, forking into the ramus posttrematicus and prætrematicus. The rr. prætrematici end in the structure with a knob, the ganglion prætrematicum, about half way up the gill pouch. The foremost of these ganglia is before the stomodæum, on a twig of the maxillaris. The small circles behind the second to the



eighth gill pouches, between the *rr. post-* and *prætrematici*, show the locations of the later appearing spiracula externa.

*Fig. 9.* *h*, hind brain; *a*, aorta; *m*, muscle; *V*, principal ganglion of vagus; *7*, seventh epibranchial ganglion; *g*, rudiment of a gang. *prætrematicum*, with which the *r. prætrematicus* is connected. Inwards from it twigs of the *r. posttrematicus*. *s*, a sympathetic ganglion; *nd*, neurodermis.  $\frac{275}{1}$ .

*Fig. 10.* *h*, mid brain; *A*, eye; *ch*, chorda; *K*, præchordal head cavity, connected by means of the hollow connecting cord with that of the other side; *m*, stomodæum; *vs*, foremost ventral spinal nerve; *ds*, foremost dorsal spinal nerve; *nd*, neurodermis.  $\frac{275}{1}$ .

*Fig. 11.* Dorsal cranial nerves of adult *Ammocætes*, *i.e.*, *Petromyzon*, semi-diagrammatic. The ganglia, especially those caudad, are somewhat separated, so as not to overlap in the figure. *A*, eye; *N*, nose; *O*, cartilaginous auditory capsule; *K*, foremost gill cleft; *I*, first, *II*, second principal ganglion of trigeminus; *III*, principal ganglion of facialis; *IV*, principal ganglion of glosso-pharyngeus; *V*, principal ganglion of vagus; *1*, first, *7*, seventh epibranchial ganglion (comp. Fig. 8); *ra*, ramus anterior; *rp*, ramus posterior; *rr*, ramus recurrens of the facialis.

NOTE.—The fractions representing the amplification of the figures are those accompanying the original. All the figures have been somewhat reduced during reproduction. —ED.

## CONTRIBUTIONS TO THE MORPHOLOGY OF THE BRAIN OF BONY FISHES.

### II.—STUDIES ON THE BRAINS OF SOME AMERICAN FRESH-WATER FISHES.— Continued. With Plates XXIV and XXV.

C. L. HERRICK.

#### B.—HISTOLOGY OF THE RHINENCEPHALON AND PROSEN- CEPHALON.

The following observations are restricted primarily to the brain of the drum, *Haploidonotus grunniens*, although also based on a study of a large series of native fishes.

In view of the novelty of many of the views presented, it should be said that great pains has been taken to verify each point, while our sections are so perfect as to make determination unusually easy. Nevertheless, in tracing unmedullated fibres like those of the callosum and hippocampal commissures, considerable uncertainty may exist respecting definite connections. Such success as we have had in a satisfactory settlement of a number of the vexed questions of the fish cerebrum may be ascribed to improved technique and constant reference to comparative data.

The cerebrum and its related structures in fishes have so long baffled investigation largely because of the failure to recognize the morphological equivalent of the cortex and a consequent misinterpretation of the cœlia. The only hope of correcting this error lay in the strict and philosophical appli-

cation of the comparative method as insisted upon and enforced by the teaching and example of Prof. Wilder, of Cornell University, and numerous European investigators.

Although Rabl-Rückhard was the first to specifically apply this method to fish brains in the satisfactory solution of the homologies of the pallium, the same identifications would have been made by any observer moderately familiar with modern comparative data. The writer independently recognized the same relations some time since, as doubtless every student of fish brains has done, whether or not his eye has met the works of Rückhard.

With the discovery that the membranous pallium is the specific homologue of the cerebral cortex of the higher vertebrates, a large field of enquiry was opened, which has thus far yielded comparatively meager results. The questions as to the fate of the commissure and tracts of the cerebrum, as well as of the cellular elements proper to the cortex, yield to none in neurology in far-reaching significance.

Before entering upon these details, I shall be but fulfilling a promise long since made in giving in detail the methods employed. In making the description as detailed and precise as possible it is by no means implied that all of these methods are the best or most convenient, or that there is any special significance in the exact proportions employed. But some experience in laboratory practice has conclusively shown that for a beginner no minutiae are unimportant, and no latitude can be safely afforded to inexperience. The formulæ and directions given in histological hand-books very generally omit what seem to their compilers self-evident precautions, on which, in many cases, the success of the preparation depends just as truly as upon the fundamental reactions involved.

It would seem to be an axiom that a method will be most generally available which combines the necessary differentiation of tissues with the nearest approximation to the perfect preservation of the essential details of each. Especially is this

true of the methods of neurological technique. It may be replied that a necessary condition of the sharp differentiation of one set of structures is the failure to develop or the diverse modification of other tissues adjacent; it may even be contended that this divergent modification is the essence of differential staining, etc. Notwithstanding this objection, we contend that for general purposes that treatment is best which brings out cells and fibres, neuroglia and nutrient tissues most nearly in their normal relations. This conclusion does not weigh against the use of special fibre stains or metallic impregnation where a specific investigation of the fibres is intended, but it suggests that such studies should be controlled by recourse to a method which shows fibres in their normal relations to cells, etc. It is also obvious that for the general purpose a stain which brings out all the cells of a given type in a uniform manner is better than a brilliantly selective stain which is also elective of one cell and not of its neighbor of the same sort. The same consideration renders a stain applied in section more reliable than one used *in toto* with the inevitable danger of affecting superficial structures more than deeper ones.

In the present case we fortunately have in a modification of methods long since familiar all that is needed for a reasonably good cotemporaneous differentiation of the important elements of the brain.

#### METHODS.

*The removal of the brain* is attended with considerable difficulty in many cases. It will be remembered that the brain of fishes is usually included in a cavity much larger than itself, and is enveloped in a large and more or less closely adherent sheath of loose adipose tissue, which separates it from the cranial walls except ventrad. It frequently is most difficult to remove the fatty mass without distorting or injuring the pallium, the dorsal sac, and the epiphysis. The great plexus of blood-vessels which is connected with

the cerebellum often offers great difficulties to orientation. If the brain be approached from above, by a cautious paring down of the head in the horizontal plane until the cavity of the skull is reached, the opening may be gradually enlarged by strong shears and the forceps, snipping away carefully with sharp scissors the membranous adhesions. The olfactory, if included, give comparatively little trouble, but, if excluded, not a little skill is required to isolate the crura and dislodge the bulb. The principal objection to this method is the difficulty of satisfactorily dissecting out the stumps of the cranial nerves. In many cases we have found it safest to remove the whole mass of fat containing the brain and pass it through the solutions unaltered. In this case the solution of the fats in the alcohol leaves cavities which become filled with vapor and are permeated with extreme slowness by the imbedding media. When they are imperfectly filled there is little hope of securing a consecutive series of sections.

It is advisable to remove some of the brains from below, in which case the jaw is carefully cut (not torn) away, taking pains not to bring to bear any tension on the nerves in the process. The opercular apparatus is then removed and the region of the eighth nerve is easily located by the appearance of the otolith sac. The opening is extended with the shears, with the precaution of cutting each nerve fibre within the cranial cavity before the corresponding area is removed. The saccus vasculosus and hypophysis are then isolated, and all the fibrous connections of one side are removed. The whole lower part of the head is cut away piece-meal until the nerve roots of the other side are reached. The cord is then severed, and, as the nerves are cut the brain is gently pushed laterad and allowed to drop into the fixing bath, without first removing the fatty envelopes.

*Fixing.*—While it is desirable that a fish brain shall be perfectly fresh, the importance of having it absolutely alive has been exaggerated. The supposed necessity of plunging it at once into absolute alcohol will account for many of the



infelicities of earlier technique. Several hours in cool weather will not materially injure a fish brain *in situ*. The medium which best fixes the brain elements in this case is a modification of Fol's chrom-acetic solution. It is prepared in a stock solution consisting of chromic acid of 1 per cent., 25 volumes; acetic acid of 2 per cent., 50 volumes; distilled water, 25 volumes. This is the generally available fluid for mammalian brains. For fishes it is reduced by the addition of an equal volume of water. Large quantities of the fluid are employed (20-30 volumes), and the brain left in it twenty to twenty-four hours. Before setting the preparation aside the utmost pains must be used to secure a natural and symmetrical position of parts, in order to orientate sections properly. For this purpose it is often of advantage to form a sling of tissue paper suspended in the fluid to lift the specimen from the bottom of the vessel and prevent flattening due to gravitation.

*Washing*.—The brain, after fixing, is suspended in large quantities of distilled water, which may be changed frequently until the yellow color disappears (about one hour usually suffices).

*Hardening*.—The brain is passed successively through 50, 60, 70, 80 and 90 per cent. alcohol, remaining twenty to twenty-four hours in each. It is of advantage in warm weather to leave in 50 per cent. spirit ten hours and then change to 55 per cent. for six to eight more before entering 60 per cent. The effect of sudden and great changes in concentration is to shrink and alter the cells.

If the brains are to be cut at once they may be passed from 90 per cent. alcohol to absolute after thirty-six to forty-eight hours, but if they are to be preserved for some weeks 85 to 90 per cent. alcohol may be used. After remaining in absolute alcohol for one day or more the brain is ready for *imbedding*. After a bath in turpentine lasting one to three hours the tissue is placed in a mixture of turpentine and paraffin, which is fluid at blood heat or a little higher temperature, for an hour or two.

For the actual imbedding, a mixture of hard and soft paraffin is chosen, which, at the temperature of the room, will cut without too great a tendency to roll. If too hard, the paraffin rolls into a close scroll, which not only is difficult to smooth upon the slide, but tends to fracture and distort the tissue. It is well to experiment on a block of the paraffin in which the tissue is to be imbedded beforehand.

For summer, a fusing point of about  $30^{\circ}$  C. is desirable. In lieu of a thermo-regulator, when the latter is unavailable, a copper plate supported on a tripod will serve to conduct the heat from the gas flame at one end to a narrow metal tray at such a distance as may be necessary to keep the paraffin just fused. The brain is suspended in the tray in any convenient way to avoid contact with the metal. Even the tinned spoons frequently used may conduct too much heat to the object. A beaker over a water bath is a simpler but less reliable method.

Care must be exercised in removing the brain from alcohol to turpentine, and in all subsequent removals, to avoid contact with (especially moist) air. The alcohol must be absolute, and should be used in sufficient quantity.

The imbedding is performed in the usual way. An oblong box is made by folding writing-paper, and a layer of the paraffin is allowed to cool on the bottom, say one-eighth of an inch thick. When this has solidified a small portion of paraffin is heated nearly to boiling in a spoon and poured into the tray, so as to partly fuse the surface of the solidified layer. This precaution prevents the flaking off of the first-formed layer. The box is then filled with paraffin from the tray containing the specimen, which is orientated carefully on the paraffin bottom, and pinned out if necessary. Generally the viscid layer will serve to hold the specimen in any desired position. When cooled, if the work has been carefully done, the whole mass solidifies about the specimen.

In cutting longitudinal horizontal sections the brain should be orientated to begin cutting from the dorson, in

order to avoid loss in orientating in the microtome. It should be remembered that the slightest overheating or contact with water may vitiate the entire process at any stage in it.

Previous to cutting the sections a dozen or so of oblong glass trays, similar to developing trays for photography, and also a narrow glass vessel about two and three-quarters inches high and two inches or less wide, are provided for the reagents. The block is fastened in the microtome and orientated, the superfluous paraffin cut away, and the block is notched at one end to enable one to determine the position of each section at a glance. A diagram of slide and intended position of section and cover is made on paper and guide pins are arranged to facilitate placing the slide. The slide is brushed over with the albumen fixative, which consists of one part of filtered egg albumen and two to three parts of of glycerine. The fluid may be indefinitely preserved by placing in the hood of the bottle a sponge moistened with a few drops of carbolic acid. It is of first importance to remove as much of the albumen as possible, as it is discolored by the stain. One may wipe gently with a soft cloth, leaving an almost imperceptible uniformly distributed film, which will nevertheless adhere to the section.

After the slide is furnished with its quota of sections, which are carefully pressed upon the slide to avoid air-bubbles, it is heated to the melting point of paraffin and cooled before passing into a tray containing turpentine. When the paraffin is completely removed the slides are drained and washed with absolute alcohol from a dropper and passed into 90 per cent. alcohol and thence into distilled water. They are then covered with the stain, which is used as dilute as possible, and allowed to stain until of a deep blue color. After washing in water, the sections are passed into alcohol, and ultimately are placed in the narrow vessel above described filled with absolute alcohol. In order not to vitiate the absolute alcohol too rapidly, the sections are flowed with it before entering the vessel. They are then cleared

in turpentine and mounted in balsam dissolved in benzole. The stain employed consists of Grenacher's hæmatoxylin with the addition of a small proportion of corrosive sublimate and ammonium chloride. Seven and seven-tenths grains sublimate and seven and three-tenths grains ammonium chloride (*i.e.*, one of Wyeth's compressed antiseptic tablets supplies a quart of the fluid.<sup>(1)</sup>)

The addition of the mercuric chloride not only acts as a preservative, but improves the stain, especially in its effect on the fibres. It remains unaltered for any length of time in any climate, but before use it should be exposed to the air in an open vessel for a number of days. Even when evaporated to dryness it may be redissolved and filtered without impairing its value. The resulting stain is a clear, transparent, purplish blue when the fluid has properly aged. The neuroglia scarcely stains, but the fibres are well brought out, and cells (unshrunk and not enclosed in vacuoles) present their characteristic structures most distinctly. The presence of acid changes the color to a purplish red, between which and the bluish tint are all gradations, depending on the exposure to air. When thus prepared, the fish brain yields to none in beauty and distinctness, and, because of the very large size of the fibres and their sheaths, forms the best subject for the study of tracts known to me.

#### RHINENCEPHALON.

In a previous paper the external topography has been sufficiently discussed.<sup>(2)</sup> In the drum, where the olfactory lobe is closely soldered to the base of the cerebrum, the former is very obviously divided into a *pes* and *pero* portion, as was, in fact, recognized by Sanders, whose description of the ichthic olfactory lobe is most detailed of any with which I am acquainted. I have elsewhere indicated the belief that

<sup>1</sup> Grenacher's hæmatoxylin is made by mixing 4 cc. saturated alcoholic solution of hæmatoxylin with 150 cc. strong ammonia alum solution in water, which, after a week or two, is filtered and mixed with 25 cc. glycerine and 25 cc. methyl alcohol.

<sup>2</sup> This journal, Vol. I, p. 217-218, p. 228-233.

these two portions are essentially different and have unlike connections, and the structure of the olfactory of fishes but strengthens an opinion primarily based on a study of Sauropsida and mammals.<sup>(1)</sup> In serpents it was shown that that so-called olfactory tract which crosses in the anterior commissure is derived from the pes or cerebral part of the bulbus, while the radix lateralis is derived from the true olfactory or glomerular structure, and it terminates in the homologue of the hippocampus or adjacent structures. This appears to be equally true of the fish, and the destination of the several tracts is much more distinctly made out than in any other group.

The pero consists of a dense investment of fibres which lie in greatly confused strands about the glomerular layer, not unlike that of all higher animals. Within the glomerular zone is an irregular layer of specific olfactory cells, which are unusually large and irregular (Plate XXV, Fig. 1). These cells are multipolar, with several long processes beside the one which enters the nerve fibre. The nuclei are small and spherical and unstained. The proximal fibres derived from this layer collect at the lateral aspect as a large and very distinct radix lateralis.

The core of the olfactory, or pes proper, is filled with a small type of fusiform cells, not unlike those of the hippocampal lobe. From this there obscurely arises the large circular bundle of the radix mesalis. The subjoined account from Sanders may be taken as applying pretty well to the case in hand:<sup>(2)</sup>

"The lobi olfactorii consist essentially of three layers. Of these the external is thicker in front, and is formed by the fibres of the olfactory nerve, which in entering diverge in all directions and form a sort of envelope for the anterior part of the lobe. More internal comes a layer of finely granular

<sup>1</sup> C. L. HERRICK, "Topography and Histology of the Brain of Certain Reptiles," JOURNAL OF COMPARATIVE NEUROLOGY, p. 24, 1891.

<sup>2</sup> SANDERS "Contr. to the Anatomy of the Central Nervous System in Vertebrate Animals," Subsection 1, Teleostei. Philos. Trans., p. 748.



neuroglia, which surrounds on the upper, anterior and lower sides a mass of small cells, which occupy the central and posterior part of the lobe. \* \* \*

“The cells of the central group are small in size, resembling to a certain extent those of the cerebrum. Many are oval or circular in outline, but generally they are more or less pear-shaped. Each cell has a nucleus of comparatively large size, which is invariably situated at the broader end of the cell; the protoplasm or cell-contents occupy the narrower side, which terminates in a more or less blunt point, from which a single free fibril emerges. The nucleus contains a single spot-like nucleolus, situated near the centre, which occasionally shows symptoms of breaking up into its constituent granules. The total average length of these cells is 0.007 millim. or 0.008 millim., their diameter 0.004–0.005 millim.; the nuclei are generally round, or nearly so, and their diameter averages 0.004 millim.

“Many of these cells occupy spaces in the neuroglia which probably correspond to the spaces surrounding the cells of the cerebrum described by Obersteiner and Bevan Lewis. Occasionally nearly the whole of the cell projects into this chamber, but more generally only the broad end, so that the nucleus alone would be bathed in lymph in the latter case. The granules, which to a great extent compose the neuroglia of the olfactory lobes, become aggregated together and form a smooth surface on the walls of these spaces; they do not actually form an epithelial layer, but seem to be a rudimentary form of that structure.

“A layer of neuroglia surrounds this group of cells, as before mentioned, on all sides except posteriorly, in which with high powers only very fine granules are to be observed. The above described cells occur very sparingly here.

“The external portion of the lobule is formed principally by the fibres of the olfactory nerve. These fibres enter at the anterior end, and occupy about half the length of the lobe; they do not go straight, but the bundle, dividing at the

apex, forms an interlacing layer, which encloses the fore part of the lobe as in a sheath, and envelops small rounded masses of coarse granular neuroglia, which may be looked upon as representing the glomeruli in the bulbus olfactorius of mammalia, described by Meynert.

"Larger cells are seen to occupy the inner edge of this layer of nerve fibres, where it begins to pass over into the stratum of finely granular neuroglia above described; at this part the neuroglia is coarser, and the cells in question occupy spaces therein in the same way that the small cells do in the central group. These cells are mostly tripolar, with sometimes one and sometimes two broad protoplasmic processes, the others being fine and probably axis-cylinder prolongations. They measure .013 millim. long by .010 broad, the nucleus measuring .007 by .006 millim.; some have a distinct spot-like nucleolus, which, however, in many specimens, cannot be so easily distinguished. Besides these, other unipolar cells occur in which the protoplasm greatly preponderates, and where the nucleus is not much larger than that of the small cells of the central group.

"In addition to the larger cells, which, as before mentioned, occupy the border of the layer of fibres, some of these fibres themselves show cell-like swellings in their course, which somewhat resemble the cells described by Meynert in the glomeruli olfactorii of the human subject. These cell-like swellings in the course of the fibres are like some kinds of bipolar cells: they have large oval nucleoli and conspicuous nucleoli."

We dissent completely from the author's views respecting the cavities within the lobe and regarding them as products of shrinkage. Especially the curious suggestion as to the origin of epithelium seems uncalled for.

The only data at hand on the development of the olfactory in fishes are meager. I quote from Holt as follows:

In the herring *at one day* (Holt, p. 480, Plate XXIX, Fig. 2, and 5 *ol.*) "the nasal sacs are closely apposed to this

region of the cerebrum, and from the ventral patch of white matter the short and stout olfactory nerves pass to the bases of the first named.

In an *early post-larval stage*, the anterior commissure is situated farther forward, and is broader than in the earlier stage. The third ventricle passes for a considerable distance in front of the commissure, and the cerebrum appears in transverse section as a vesicular mass with dorso-lateral patches of white matter; from the latter the olfactory nerves pass forwards and outwards to the nasal sacs, now removed some little distance from the cerebrum and disposed partly in front of it.

In the *stage one-half-inch long*, the cerebrum has undergone a further upward rotation, and the olfactory lobes are now seen as bulbous masses projecting from the front end. From the anterior ventral edge of each lobe the olfactory nerve passes toward the nasal mucous membrane. Each olfactory lobe consists, histologically, of fibrous matter, with a few scattered deeply staining cells, and a narrow peripheral margin. It is constricted at its point of origin from the cerebrum, as in later stages, but its height is as yet insignificant.

In the *stage three-fourths inch long*, the olfactory lobes are more elongated than in the last stage, and the constriction at their point of origin is better marked. A transverse commissure unites their bases. The olfactory nerves turn outwards.

[The commissure above mentioned can hardly be other than that we have identified with the corpus callosum.]

Upon the general question of the nature of the olfactory lobe and fibres, the following remarks are quoted from Kölliker:<sup>(1)</sup>

“In my studies upon the development of the organs of smell in human embryos<sup>(2)</sup> I discovered that the olfactory,

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<sup>1</sup> KÖLLIKER, A., “Ueber die erste Entwicklung der Nervi olfactorius,” Sitzungsberichten der Würzburger phys. med. Gesellschaft, 1890, XIV Sitzung von 12. Juli.

<sup>2</sup> KÖLLIKER, A., Festschrift für Zürich, 1883.

unlike all other nerves, in the earliest stages consists throughout their entire extent of nucleated bundles of the finest parallel fibrils, which bundles I compared with the axis-cylinders of other nerves. From this circumstance I concluded that these nuclei correspond to the nuclei of nerve cells, and that a nucleated sheath of Schwann accordingly is not present, although it has been assumed by all authors since Max Schultze. If this were correct, then the olfactory fibres consist of bipolar nerve cells, which either each sends a process peripherad, or, as seemed to me probable, are united in moniliform series, as must be assumed in the sympathetic; in this case the nerve grows by successive subdivision of the nucleated portions without complete separation of the resulting segments.

“In any case the development of such a nerve from the central nervous system is difficult to explain from any existing analogy, and it afforded a very desirable solution of the matter when His, a short time since, announced that the olfactory does not develop from the olfactory lobe, but rather takes its origin from the epithelium of the olfactory pits, and grows in the centripetal direction, like the cells of the spinal ganglion. This investigation of His I have recently verified with the following results:

“In the earliest stages the olfactory pits have no nerves, and are not connected with the olfactory lobe. In an embryo chick of four days there is a slight proliferation of the epithelium of the olfactory at the end nearest the brain only, forming a bundle .030–.054 millim. thick, which can be followed to the outer margin of the hemisphere without entering into any connection therewith. The bundle is finely fibrous and nucleated, and exhibits on its surface fusi-form cells.”

Prof. Kölliker records similar observations upon mammals and concludes:

“I consider the assumption made by His as very probable, and may add that when the olfactory nerve has once

entered the bulbus the latter acquires, even in the embryo, a very peculiar appearance.

“As regards the anatomical significance of the elements of the olfactory nerve, His regards them in the embryonic state as bipolar nerve cells, and the nerves themselves as the olfactory ganglion. Furthermore, he states that the greater number of these cells can be re-identified later in the olfactory lobe itself. These cells, inasmuch as they were originally epithelium of the nasal pit, have undergone a considerable migration, so that the question naturally arises whether all the nerve cells of the olfactory ganglion have not gradually entered the bulbus. The solution of the question depends upon the interpretation of the histological structure of the olfactory nerve of the adult. If the nuclei of the olfactory belong to the nerve fibres, then the peripheral portion of the olfactory is to be regarded as the ganglion; if, on the other hand, these nuclei belong to the sheath, it may be assumed that all the ganglion cells have entered the bulbus.

“In this discussion His has overlooked my statement, made in 1883 and based on the investigation of a human embryo of the second month, ‘that the nucleated fibrillated bundles of the olfactory nerve of embryos are the direct forerunners of the nucleated pale olfactory fibres of the adult, and therefore are to be compared with the axis-cylinders of other nerves and the nuclei with the nuclei of nerve cells.’ Nevertheless, these elements differ from those of a typical ganglion in that each olfactory fibre possesses a number of nuclei, and therefore corresponds to a considerable complex of nerve cells. The mitotic figures found in olfactory fibres of the rabbit show that the bipolar cells of the olfactory nerve do not grow into the bulbus, but extend in length in such a way that with the increased length of the fibre the nuclei multiply, so that finally there results a peculiar long, multi-nucleate nerve cell, which can only be compared with the sympathetic.



"If we assume that the sensory peripheral fibres terminate in free branches in clusters of gray matter, and that from the cells of such niduli new nerve fibres arise and conduct the excitement centrad, the conditions for determining central tracts and centres are satisfied."

In 1854 Kölliker described the olfactory fibres of the ox and sheep as tubes with nucleated contents.

The above view, which is theoretically so probable, receives considerable confirmation from the facts to be presented, as well as a partial new interpretation.

A glance at Fig. 1, Plate XXIV, will show that the radix lateralis passes directly and without interruption to a special caudo-ventrad projection of the cerebrum, already identified upon topographical grounds as the homologue of the hippocampus (see previous paper of this series). There the fibres end near a special zone of cells. Entad of this specific homologue of the hippocampal cells a tract of non-medullated fibres seems to arise, which passes cephalo-ventrad and crosses to the opposite side immediately caudad of the callosum. This fibre tract can be nothing else than a rudimentary hippocampal commissure, together with the fornix. That the latter structure is included is shown by the fact that a small branch passes to a bifid cellular mass projecting into the ventricle from the caudo-ventrad aspect of the callosum; in other words, an unmistakable homologue of the body of the fornix. To complete the identification, we think we find a small tract extending from the latter to the thalamus. The unmedullated nature of the fibres makes the study difficult.

The radix mesalis pursues an altogether different course. After entering the post-rhinalic region of the cerebrum, this cylindrical bundle passes caudo-mesad, and, after dividing into a number of smaller tracts, forms a part of the præcommissural system. Nevertheless, this band is distinct from both the true præcommissura and the axial commissure or decussation beneath it.

In assuming an entirely distinct function for the two radices and the structures supplied by them, we meet an apparent difficulty in the fact that in those fishes whose olfactory bulb is exerted the radices are both produced from the cerebrum in the elongate crura. It must be remembered, however, that we have already shown that in these cases the ventricle continues out with the radices, so that, morphologically at least, the bulb contains even in this case a part of the cerebrum, *i.e.*, a distinct pes.

#### PROSENCEPHALON.

The study of the cerebrum of fishes is likely to furnish the best and most convenient basis for determining their position among the classes of vertebrates. The skeleton is less trustworthy than usual, by reason of its specialized nature. The development of a vast number of membrane bones, with the marvelous changes in the whole bodily configuration and structure dependent thereon, can, at most, only be regarded as superficial characters as compared with those entirely independent changes in the brain within a spacious cavity shielded from all direct external influences.

Accepting the fundamental homologies laid down by embryology, our morphological study proceeds from a condition when the prosencephalon consists of a single dilation of the neural tube, the primitive prosencephalic vesicle. Any attempt to construe vertebrate brains which fails to recognize this primary *undivided* and *closed* character of the cephalic cavity must fail. It is possible for the requisite increase in cerebral substance to be produced in at least three different ways. First, there may be developed from the sides of the tube thick excrescences in which cells may proliferate. Second, the vesicle may increase in size as a whole, retaining its undivided character. Third, the vesicle may enlarge in certain portions, while elsewhere it may retain its simple original form. In Teleosts the first and the second methods chiefly prevail in contrast to the higher vertebrates, where

the first and third methods maintain. In regions of the neural tube farther caudad there are two sets of commissures, one lying in the dorsal and the other in the ventral wall of the tube. These remain in their primitive form in the cord.

The question now arises, to what extent the same relations persist in the cerebrum. In fishes, since the cortex is anatomically absent and simply morphologically represented by the pallium, it is obvious that the cells and commissures are either absent entirely or represented functionally by structures in other parts of the primary prosencephalic vesicle. Theoretical considerations, as well as such evidence as we have from embryology, show that the tendency of development in the cerebrum proper is dorso-caudad, *i.e.*, the outgrowths of the primitive vesicle are reflexed and tend to overlap the axial portions caudad. This is also the case to a certain extent even in the growth of the pallial sac in fishes, but since the latter does not contain nervous elements, such revolution cannot change the position of the commissures, etc., belonging properly to the roof. Following this clue as given in a previous article,<sup>(1)</sup> it has been possible to determine the relations of all the important tracts, commissures, and niduli of the cerebrum, including æsthesodic and kinesisodic niduli, corpus callosum, fornix, hippocampal commissure, fornix body, and hippocampus, in an unexpectedly simple way. When we remember that the cortex of higher vertebrates contains those centres whose functions associate them most closely with conscious acts, and that it is regarded as the true organ of consciousness, including all the higher faculties, it becomes of great interest to discover whether the axial lobe of fishes contains cell clusters which can be looked upon as the physiological equivalent of the cortical areas of higher animals.

The writer, in a series of publications covering most of

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<sup>1</sup> C. L. HERRICK, "Topography and Histology of Certain Ganoid Fishes," JOURNAL OF COMPARATIVE NEUROLOGY, Vol. I, p. 167, June, 1891.

the major divisions of vertebrates, has striven to show that there is a constant difference in form between the kinesodic and æthesodic cells. On this basis areas are marked off more or less distinctively associated with one or the other function. It was noted that the two kinds of cells are more distinctly segregated in lower vertebrates, while in higher types there is a greater tendency to inter-blend and form complex clusters. In other words, there is a very obvious anatomical basis for the assumption of more complex inter-action between afferent and efferent excitements in the cortex of higher vertebrates.

If the fish is not purely reflex and automatic in its reactions, some substitute for the undeveloped cortex must be found, and would be sought for in the only remaining part of the cerebrum, *i.e.*, the axial lobe. As we have seen, the axial lobe of Sauropsida is certainly much more than the homologue of the striatum of mammals. The writer endeavored to show that in alligator and other reptiles there are definite proliferating areas, which may be regarded as centres of origin for the cortical niduli.<sup>(1)</sup> Mr. Turner has observed the same appearance in birds,<sup>(2)</sup> and his studies make it probable that in that group, where the cortex is greatly reduced, its loss is substituted for by involuted cell niduli of cortical origin, but buried within the axial lobe. This forms an important clue in the search for the homologues of sensory and motor areas in the fish.

In general, then, we believe that the fish cerebrum is derived from a primitive type in which the primary prosencephalic vesicle had scarcely, if at all, developed lateral (or definitely cerebral) structures; that most teleosts have arisen from types which possessed a slightly developed cortex, but that an increase in the size of the head without the commen-

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1 "Notes on the Brain of the Alligator," Journ. Cin. Soc. Nat. Hist., Vol. XII, p. 455; "Topography and Histology of the Brain of Certain Reptiles," JOURNAL OF COMPARATIVE NEUROLOGY, Vol. I, p. 21.

2 C. H. TURNER, "Morphology of the Avian Brain," JOURNAL OF COMPARATIVE NEUROLOGY, Vol. I, p. 71.

surate development of cranial walls forming a direct support for the cortex has resulted in the gradual limitation of the nervous matter within the axial lobe leaving only the pallium to represent its former position; that the cell structures proper to the cortex are contained in the axial lobe, which is, accordingly, more complex than that of any other group of vertebrates; that the two types of æsthesodic and kinesodic cells are as distinct in fishes as in reptiles; that these cells are grouped in distinct areas and may be classified into minor divisions, based on size, etc.; and that the commissures and tracts sustain much the same relations to these clusters that they would if the latter lay in a cortex cerebri instead of the axial lobe. Of the above conclusions, the suggestion as to the cause of the suppression of the cortex is a mere guess, incapable of serious attempt at demonstration; the others seem to me well supported by the facts at hand. It is obvious that one result of this peculiar limitation of the cortex is to largely interfere with a free and generous development of the organs of consciousness and spontaneity. A fish would be handicapped in any competition with animals whose cortex would permit of easy increase by centrifugal growth or by infolding and plications.

In a preceding article it was shown that the axial lobe of fishes is marked by deep and more or less constant fissures separating topographically several lobes or areas. It remains to show that each of these lobes has its own peculiar cell structure and fibre connections, warranting the assertion above made, that the axial lobe of a fish is more complex than that of other animals, not even excepting the bird. Before passing to the special description, reference is made to the useful paper by Edinger, in which a great deal of useful comparative matter is collected and discussed in the light of recent literature.<sup>(1)</sup> The statement on page 106, that "the amphibian brain is the simplest brain which is

1 EDINGER, DR. L., "Untersuchungen über die Vergleichende Anatomie des Gehirns," I.; "Das Vorderhirn," Abhandl. Senkenbergischen naturf. Gesellschaft, 1888.



found in the vertebrate series," should be understood in some other than the phylogenetic sense probably, for even a more highly differentiated brain in which the primitive simplicity of the prosencephalic vesicle is preserved may be believed to indicate a more primitive origin.<sup>(1)</sup>

In order to get an idea of the histological differentiation of the axial lobe, we may first examine a horizontal section somewhat dorsad of the anterior commissure (Plate XXIV, Fig. 2). The anterior commissure fibres are situated near the median margin and are spreading out dorso-laterad in the mesaxial lobe. The actual crossing of the fibres takes place in the præthalamus or a projection from its dorsal aspect. The fibres of the anterior commissure proper pass laterad into the central lobe, beyond which they were not followed. The central lobe is occupied with the numerous bundles of the peduncles around which are grouped niduli of large pyramidal cells such as are commonly found in motor areas of higher animals. The processes are long and subdivide. The apical process is usually peripherad. The nuclei are small and densely stained. The entire cell stains more deeply than other adjacent elements. A spur of such cells follows the callosal fibres toward the meson (Fig. 2, Plate XXV). The whole cephalo-lateral aspect is occupied by the *lateral*, or *parietal lobe*, the cells of which are of the æsthesodic variety. From the frontal part of the mesaxial lobe it is separated by a distinct frontal fissure, as it is from the cuneus by the Sylvian fissure. From the central lobe it is separated by a thin tract passing obliquely dorso-cephalad and laterad, *i.e.*, radiating toward the periphery. From this tract, which extends from the frontal fissure cephalad to the

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<sup>1</sup> It is interesting to see that Owen has arrived at a conclusion similar to the above on the basis of external form and gross dissection, as may be gathered from page 286 of the first volume of his "Comparative Anatomy," especially the following paragraphs: "It is interesting to perceive on the superficies of the solid prosencephalon in many fishes the foreshadowing of the convolutions, which are not fully established until an advanced mammalian grade is attained. The prosencephalon of the fish is far from being a miniature model, but it may be regarded as the potential representative of the complex cerebral hemispheres of man."

Sylvian caudo-laterad, isolated fibres and small tracts pass toward the periphery nearly in the plane of the section. The peripheral or ventricular border of this lobe is clothed with a single-layered epithelium, from the apices of the cells of which fibres extend long distances entad, as in the brains of Sauropsida. The cells of the lateral lobe (Plate XXV, Fig. 6) are fusiform, with clear spherical nuclei of large size. The protoplasm is faintly stained and the processes are short. The cells are similar to those found in æsthesodic areas of the cortex in reptiles.

The *cuneus* consists of concentric layers of smaller fusiform cells. Near the surface, however, is a small zone of cells like those of the lateral lobe, or nearly twice the size of those composing the bulk of the lobe. Dorsad this lobe borders upon the occipital, and caudad it is separated from the temporal and hippocampal.

The *occipital lobe* merges insensibly into the temporal ventro-laterad, but extends cephalad a long distance upon the dorsal aspect. In the present region it is difficult to say which is cut.

The *mesaxial lobe* occupies the whole mesal aspect, and is divided into a cephalic and caudal portion by a fissure in the mesal surface. This may be the homologue of a fissure mentioned by C. Judson Herrick in the cat-fish.

The cellular elements are small and vary considerably. Cephalad of the above fissure, which may be called splenial for convenience, and caudad of the callosal tracts, is an area where numerous small fusiform cells are closely massed. Caudad of the splenial is a region where there is a mixture of the above described and narrow deeply stained pyramidal cells resembling the so-called rhinomorph cells. A similar sort of cells occupies the tract caudad of the peduncles in the central lobe (Fig. 4, Plate XXV). Cephalo-mesad of the pyramids at this level is a dense clustre of small fusiform cells, with a slight admixture of pyramidal elements. A section at the dorsal level of the callosum is figured in Plate XXIV, Fig. 2, and requires no special description.

Some distance dorsad of the section first mentioned, a strong projection of the central lobe passes toward the caudal surface and is interposed between the temporal below and the occipital above. The cells are small pyramids, staining very deeply. There are similar projections along the frontal fissure. Thus, while the pyramidal cells are central, they are connected with the surface of the axial lobe at several points. The *occipital lobe* dorsally contains flask cells simply, and forms a cap over the one just described.

In longitudinal sections the caudad projection of the pyramidal cells of the central lobe is seen to be accompanied by a strong tract. Although the details of these arrangements would be interesting, it is intended to reserve them for a wider range of comparison.

The *temporal lobe* merges ventro-mesad into the hippocampal, both of which contain small flask cells, with clear spherical nuclei and inconspicuous processes.

The specific representation of the hippocampal niduli is a mass of somewhat smaller and more deeply staining cells, forming a layer near the caudal margin of the lobe, into which the fibres of the radix lateralis may be traced. These cells are grouped in clusters, and are essentially bipolar or flask-shaped.

The ventral projection of the mesaxial lobe terminates cephalad in the bifid body, which is here recognized as a probable homologue of the corpus fornicis, and caudad of the latter in a gradually diminishing area cephalo-ventrad of the anterior commissure, perhaps homologous with what I have termed the prærhinalic lobe in mammals. Both these areas abound in small, dark-colored and spherical nuclei, like those of the blood corpuscles, and clearly homologous with the so-called Deiter's corpuscles. There are less numerous flask cells of the smallest size.

The tracts and commissures of the cerebrum complete in a very satisfactory way the chain of evidence begun above. The callosum of fishes was first correctly identified, I believe,

by the writer as indicated above.<sup>(1)</sup> Previous writers have either regarded it as absent or fused with the præcommissura. In the latter view, proposed and defended by Osborn, the present author coincided for a time, in spite of the grave morphological objection that the callosum and hippocampal commissure on the one hand and the præcommissural system on the other belong to distinct systems. The former are cortical, the latter basal. It would be necessary, in a case like that of fishes where the cortex is suppressed, to consider that the axis of the cerebrum had been greatly modified and shortened in order to bring the two systems into juxtaposition. No such supposition is necessary, for the callosum and fornix systems are present and in just the position which the nature of brain development would lead one to predict, *i.e.*, well forward near the union of pallium and axial lobe, in close relations to the lamina terminalis and on the opposite side the axial part of the ventricle from the callosum. Fig. 8, Plate XXV, illustrates the relation. A glance at Fig. 2, Plate XXIV, will indicate how distinct the two systems are. It will also be noticed that the callosum is intimately associated with the pyramidal cells of the central lobe, which we insist upon as representing suppressed motor cortical areas. Immediately caudad of the callosum are two cellular projections into the ventricle, which in all respects represent the corpus fornicis. A tract homologous with the combined fornix and hippocampal commissure springs from the hippocampal cells entad of the radix lateralis and passes to the median line, part entering the fornix body and part form a commissure caudad of but adjacent to the callosum. There is a cellular interval between the two commissural systems. There is a small tract arising in the fornix body of either side destined for the thalamus.

In the second part of Professor Osborn's valuable paper on the corpus callosum<sup>(2)</sup> these words occur: "In regard to

1 JOURNAL OF COMPARATIVE NEUROLOGY, pp. 164-168.

2 Morphologische Jahrbuch., Band XII.

other groups of fishes [than Dipnoi], I still adhere to the hypothesis that the commissura interlobularis is a primitive form of the whole transverse commissural system of the hemispheres, thus representing both the anterior commissure and the callosum."

The facts above presented, while they seem to disprove this position, serve to establish only the more firmly the philosophical theory founded by Osborn, by which the structures above referred to are homologized throughout the vertebrata.

The so-called anterior commissure consists of three parts, viz., a true commissural band connecting the two sides of the base of the cerebrum; second, the decussation or commissura of the radix mesalis olfactorii; third, the axial commissura, first described by Edinger as the commissure of the basal cerebral fasciculus. He says:<sup>(1)</sup> "Diese commissur kommt in allen Tierklassen vor, is aber bis jetzt nur einmal, von Osborn gesehen worden, bei Reptilien. Mit der Commissura anterior (com. interlobularis, autt.) darf sie nicht verwechselt werden, sie liegt weiter hintern und gehört bereits der Zwischenhirn an. Es ist mir fraglich ob sie eine Commissur oder eine Kreuzung einzelner Bündel darstellt." The commissure is of considerable size, and is closely associated with the commissure of the radix mesalis.

The *peduncles* consist of three portions or bundles.

The basal cerebral fasciculus, the decussation of which is above noticed, was seen in ganoids and described as forming a part of the anterior commissure.<sup>(2)</sup> In the drum it is entirely distinct from the lateral motor and sensory tracts (only the latter was included in the description just referred to). This decussation lies between the præcommissura and the decussation of the radix mesalis, and, after crossing, the fibres may be traced some distance into the thalamus, passing on

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1 EDINGER, DR. L., "Untersuchung. u. d. vergl. Anat. des Gehirns," I; "Das Vorderhirn," 1888.

2 HERRICK, C. L., JOURNAL OF COMPARATIVE NEUROLOGY, Vol. I, p. 169.



its way the dense nidulus of multipolar cells which is so conspicuous a feature of the ventricular aspect of the thalamus.

The ventro-mesal portion of the peduncles proper seems to have a different course, both in the cerebrum and the thalamus, from the dorso-lateral portion. The former pass cephalad and mesad and give rise to the thin disperse tract which separates the lateral from the central lobe. Many of its fibres cross in the callosum. The latter forms the conspicuous peduncular tract occupying the posterior part of the central lobe. Its fibres appear to supply the dorsal and caudal parts of the axial lobe.

#### PLATE XXIV.

Horizontal longitudinal sections through the entire brain of the drum, *Haploidonotus*. Those parts especially referred to in this instalment are, for the most part, named on the plate. The left side is at a slightly more ventral level than the right.

*Fig. 1.* Section through the olfactory lobes and corpus fornicis. The radix lateralis is easily followed throughout its entire length from the lateral aspect of the pero to the hippocampal lobe. The radix mesalis arises in the pes, and, curving ventrad and then dorsad, appears cepalo-ventrad of the axial commissure as a circular bundle.

*Fig. 2.* Section at the level of the axial commissure (see text) and callosum.

*Fig. 3.* Section above the level of the præcommissura, whose tracts are nevertheless seen in the section. The index letters indicate regions from which the detailed drawings of histology were taken as given on Plate XXV.

*Fig. 4.* Section near the dorsal surface of the cerebrum. The figure illustrates the structure of the volvula and cerebellum. Compare Fig. 7, Plate XXV.

#### PLATE XXV.

*Fig. 1.* Highly magnified portion of the pero entad of the glomerules. There happen to be no instances of direct connection of cells with glomerules in the field.

*Fig. 2.* Pyramidal kinesodic cells from central lobe (see Fig. 3, Plate XXIV).

*Fig. 3.* Superficial part of lateral lobe to show epithelium. The æsthesodic cells of that region are cut transversely.

*Fig. 4.* Peculiar cells in tract *e*, Plate XXIV.

*Fig. 5.* Portion of cuneus to show both sorts of flask cells. The outermost properly are associated with the cells of the lateral lobe.

*Fig. 6.* Normal æsthesodic cells of the parietal lobe.

*Fig. 7.* Longitudinal perpendicular section through the entire brain.

*Fig. 8.* Section just dorsad of the olfactory crus to show the course of the fornix tracts and the callosum.

*Fig. 9.* Longitudinal section of cerebrum somewhat dorsad of that of Fig. 3, Plate XXIV.

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#### EDITOR'S ANNOUNCEMENT.

The editor hoped to be able to announce in this number the result of preparations now making for greatly improving and extending the scope of this journal. Inasmuch as he is about to be absent in Europe for some months, the place of publication *ad interim* cannot be definitely announced, but all correspondence should be directed to Granville, Ohio. An extra number will be issued in January, 1892, and the regular March issue will perhaps be somewhat delayed. On the other hand, our readers are assured that the volume will be made more comprehensive and valuable than the present one.

Among the articles for the ensuing year will be a descriptive sketch of the neurological students and laboratories of Europe, and the "Development and Histology of the Thalamus."

The coöperation of the ablest specialists in Europe and America is expected. The department of Comparative Psychology will receive special attention.

After October, 1892, the JOURNAL will be issued regularly from the University of Chicago.



Fig. 1.



Fig. 2.

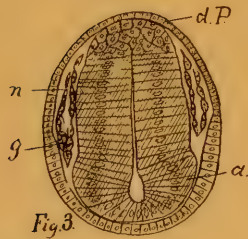


Fig. 3.

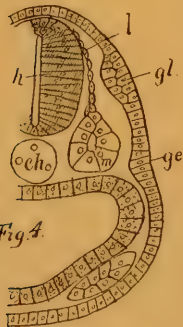


Fig. 4.

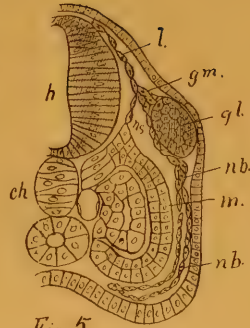


Fig. 5.

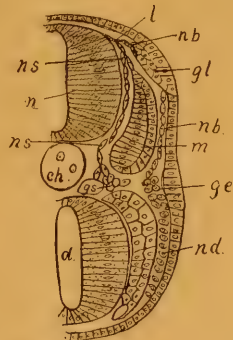


Fig. 6.

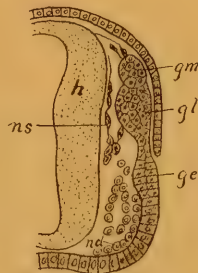


Fig. 7.

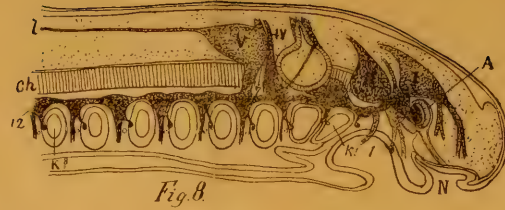


Fig. 8.

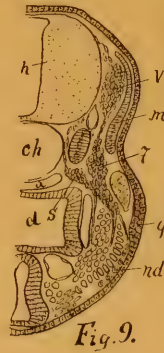


Fig. 9.

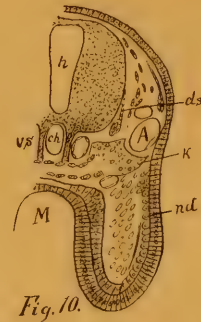


Fig. 10.

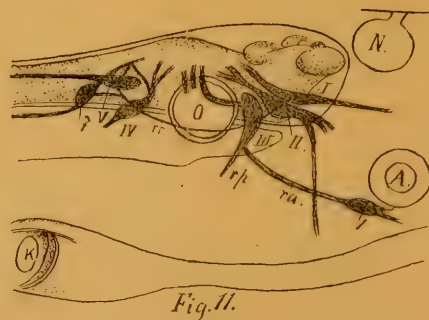
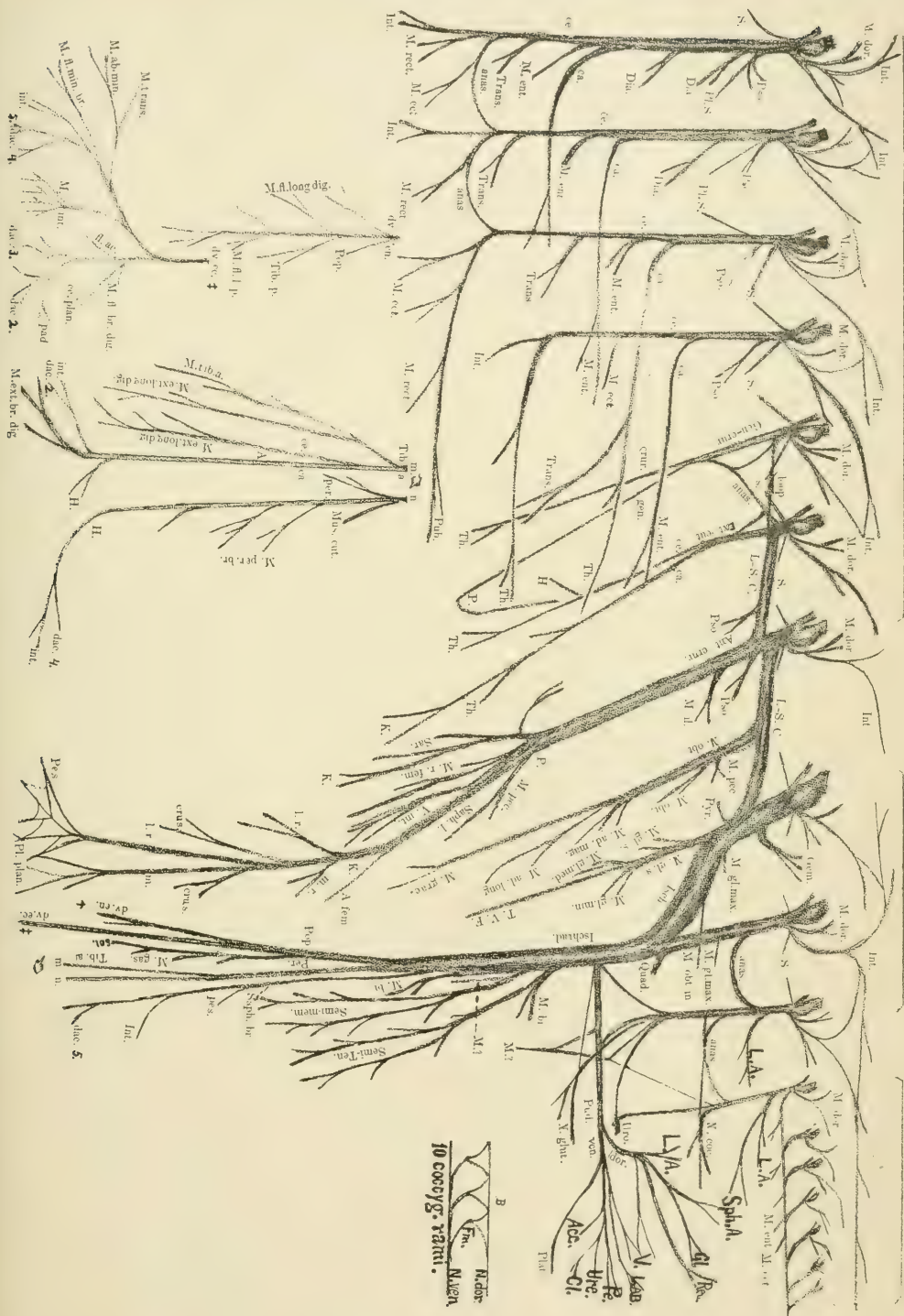


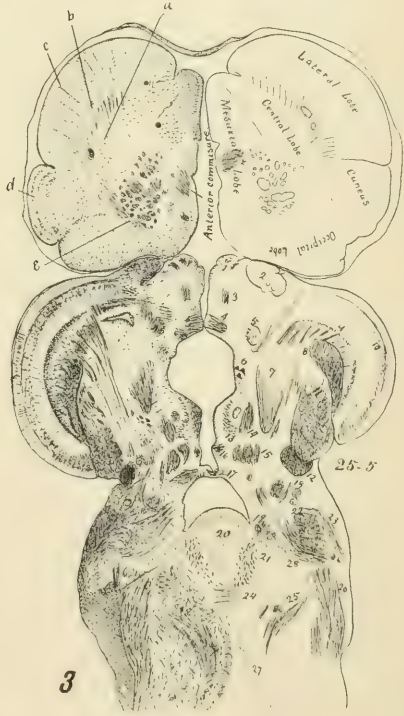
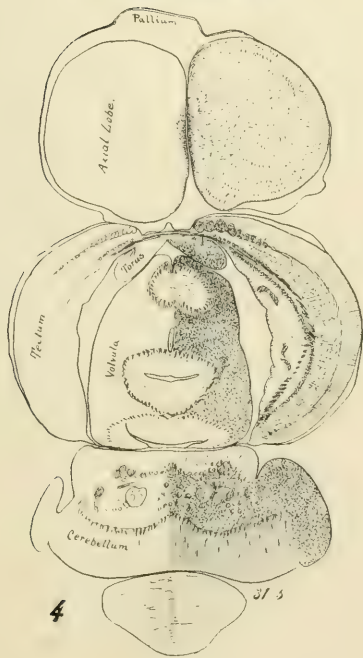
Fig. 11.



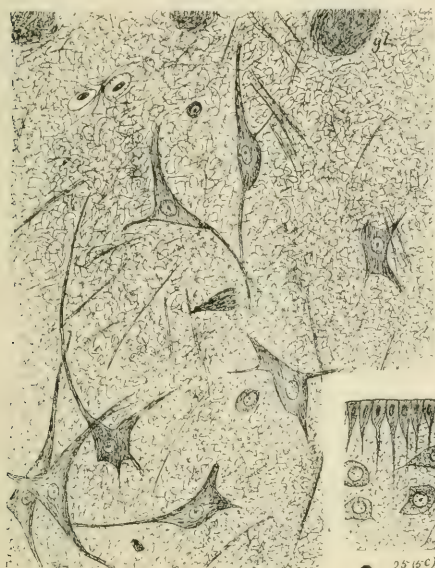










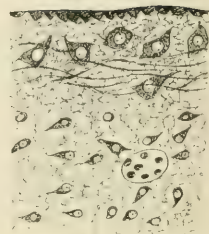


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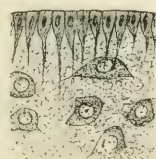
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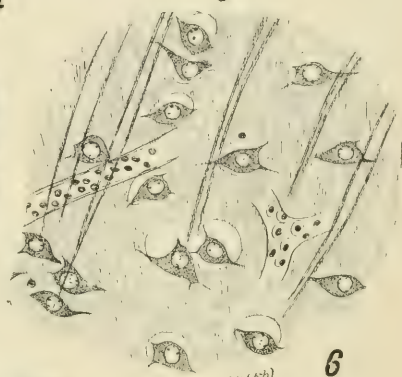
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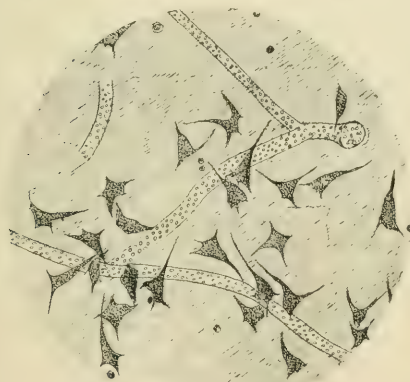
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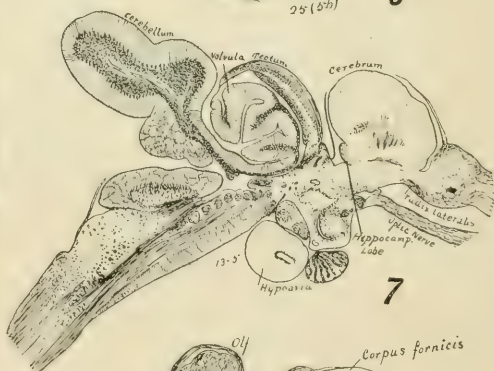
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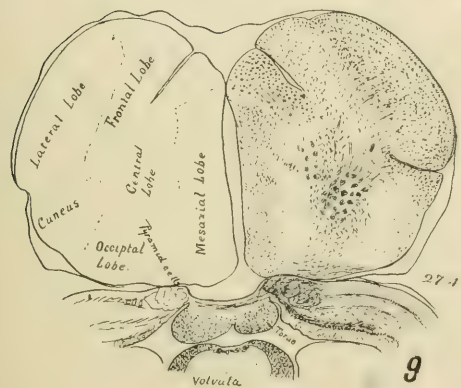


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## THE NEURASTHENIC FACTOR IN THE DEVELOPMENT OF MENTAL DISEASE.

A. B. RICHARDSON, M. D., Superintendent of the Columbus Asylum for Insane.

To have an intelligent conception of the relation of nerve exhaustion to the development of mental disorders it is necessary to learn something of the manner in which the brain cells receive their nutritive supply and how the products of their physiological activity are removed. We will assume that the cells of the cerebral cortex are the chief organs concerned in the evolution of mental phenomena, and that a study of the physical basis of mind is a study of these microscopic bodies, their connections, supports, sources and methods of renewal and the manner of their riddance of waste and deleterious products. After these have been as fully investigated as the facts at hand will permit, we will then be in position to investigate in what manner they are disordered in the various stages of the development of mental disease, and I have chosen the name which heads this paper because I believe it wise to impress the fact that these incipient changes are in every instance such as cause errors in the nutrition of the cell elements and derange the normal balance between their supply of assimilative material, on the one hand, and the demands made upon their stores of energy, on the other.

The histology of the cells of the cerebral cortex has been carefully studied of recent years. Many useful facts have been established, but much remains more or less uncertain. We shall not attempt a review of this further than to describe their relations to the other constituents of the cortex.

The brain cells of the cortex lie imbedded in a soft matrix of delicate branching cells, composed of numerous branching fibrils from a small central focus, which entwine in all directions and form a most delicate cushion for the support of the more highly developed brain cells. Their uses seem to be those of support of these cells and possibly a share in their nutrition.

The brain cells, proper, are connected with the exterior and with each other, by both direct and indirect methods. They have two or more branching fibres or poles, through which their connections are effected. Some of the cells have a basal process which does not diminish in size and has in some instances been connected directly with an axis cylinder of an efferent nerve filament. The other processes diminish gradually in size by subdivision until it is very difficult to trace them to their termination. They seem finally to form a delicate matrix of fibrils, and many of the cells have no distinctive processes other than those which form this matrix. From the aggregation of the fibrils of this matrix on its ventral side larger fibres arise which have been traced into the axis cylinder of other nerve fibres. Whether or not this difference in the connection of the brain cells with the axis cylinders of the nerve fibres indicates a different function in the two classes, is not well determined, but analogy would indicate that it does so, and it has been assumed that the direct connection is with efferent nerve fibres and the indirect with afferent fibres.

The blood vessels to the central cortex are exceedingly delicate in structure and are susceptible of great variation in diameter. In the capillaries the various coats disappear, leaving the endothelial lining alone, and this is quite delicate in structure.

The blood vessels lie in a lymph space, which is much larger than the diameter of the vessel and is probably lined with a delicate membrane which closely invests the brain tissue. About the brain cells there is a similar lymph space and these perivascular and pericellular lymph spaces have been seen to be connected by lymph tracts or clefts in the brain substance, which thus afford a direct drainage of the cell surfaces into the great lymph reservoirs between the membranes of the brain. Along the course of the vessels and in the neighborhood of the cells, most delicate and almost undiscoverable (in the normal state) cells are found which are sometimes connected to the vessel and reach out toward the cell elements. In pathological states these become much more visible, increase in size, are more readily stained, and become filled with the products of cell degeneration.

These anatomical data will enable us better to understand the pathological changes which are found in incipient mental disorders and to note the connection which they have with the problem of nutrition. Still beyond our vision lies the field in which the connection is made between mind activities and the brain elements, and the seeming impossibility of the solution of this problem has necessitated the introduction of theory in the treatment of the subject of mind disorder; but theory is often admissible as a basis for guidance in therapeutics or prophylaxis and for such purposes we shall not hesitate to use it when full investigation partly fails.

The primary steps in the development of mind disorders would seem to be dependent upon the following anatomical, physiological and pathological data: (1). The capacity of the cell elements of the cerebral cortex to assimilate nutritive material varies in different types of cells as found in different organisms, and in some is defective. (2). That susceptibility of these cells to impressions, which gives them their functional power, is possessed by different types in varying degree and in some is excessive and out of proportion to the assimilative capacity of the same cells, in others is deficient. (3). That delicate poise of functional power in the brain cell, which, on the one hand, enables it to react to impressions, and on the other gives it the power to restrain, inhibit and direct the results of these impressions, is possessed by different types of cells in varying degree. When deficient in delicacy it results in defective capacity and the nutritional errors which are due to inactivity. When the normal power of reaction is present but the power to inhibit and direct is deficient, excessive reaction, and particularly such as is disproportionate to the supply of nutritive material assimilated by the cells, leads to serious cell degeneration.

It is only by some such terms as these that we can intelligently explain in physiological language the transmitted, congenital or acquired tendency toward mental derangement. The want of balance in the brain cell between its capacity and opportunity to assimilate nutritive supplies, on the one hand, and its susceptibility to impressions and its power to exercise inhibitory control of its energy, on the other, is handed down from defect-

ive parentage, is the accompaniment of arrested development, or is the penalty left by previous disease.

As the result of the first of these causes, to-wit, the capacity of the cell to assimilate nourishment, some types of cells have a very limited functional capacity, within the limits of safety, and slight power of resistance. They are easily overworked and their possessors constitute oftentimes the mental invalids which abound to enliven the tedium of the busy practitioner. Still other types of cells are essentially short-lived, coming early to maturity, possessing their maximum of functional power for a comparatively short period, and soon falling into decay and the degeneracy of premature old age. Hysteria is an excellent example of a form of mental disorder due to the third class of cell defects, and has its origin in defective inhibitory control of cell energy. That recovery from mental disease is so seldom satisfactory, and the tendency toward recurrence after one attack is so great, is due to the changed nutrition of the brain cells and their diminished capacity to assimilate nourishment. It is to be borne in mind also that the large lymph spaces around the blood vessels of the brain and about the brain cells, and the connection seen between these in some cases, at least, indicate the importance which we must attach to the rapid elimination of waste products from contact with the cellular elements. The products of cell-metabolism are extremely inimical to the normal activity of the cells, and their toxic effects upon the system have been fully established.

To understand more clearly cell nutrition and cell energy and their delicate adjustment and interdependence, we must remember that there is an extreme susceptibility in these carrying blood vessels, to stimulation from the activity of the cells themselves, and that their calibre and the supply of material which they convey, vary with the slightest variation of cell activity, or their stimulation from the exterior. With this varying calibre and the consequent changes in the blood pressure come the modifications in the relation which the nutritive supply bears to the activity of the cell. There is a genuine hyperaemia of the brain cortex during its period of activity, which seems essential to the rapid evolution of energy, and during which both the amount of nourishment consumed and of waste products pro-

duced are increased. During the periods of quiescence in cell activity, the blood pressure is diminished, the amount of nourishment sent to cells is lessened and the waste products diminished, yet it is then that the cells store up energy because their activity is almost nil and the balance is far on the credit side of the account.

Reasoning from these data, then, we see that the incipient variations in cell nutrition and consequent mental derangement, come from two sources, the first those that diminish the amount of material assimilated by the cell, the second, those that increase the demands made upon it. The first of these may be induced indirectly by a diminution in the amount of the blood or a deterioration in its quality. In such states there is an anaemia of the brain cell, in some cases, and, in others, a passive hyperaemia, the result of a want of proper tonic in the vessels. Much oftener, however, the diminution in the nutritive supply depends upon a genuine hyperaemia of the cortex. The increased pressure of this, which is either excessive in degree or continued beyond the normal limit, prevents the healthy transfer of nutritive material through the vessel walls. The cause of this abnormal hyperaemia is usually the over stimulation of the cells themselves. This of itself endangers the safety of the cells by increasing their requirements for nourishment. It is impossible to separate the effects of these two causes. Overstimulation of the cells accompanies the thousands of exciting causes of mental disorder. None, however, is more effective in its production than worry. Whatever may be its origin this induces a rapid destruction of tissue in the cerebral cortex. There is a prolongation of the normal hyperaemia, and an inability of the vessels to contract upon their contents with the normal diminution in their stimulation, due to exhaustion and paresis of their nervous control. It is not difficult for any one to test this in himself. Apply yourself to intellectual work which is felt to be a strain on you and continue this to an hour beyond that usual for your retirement. You will notice how difficult you will find it to settle your brain for repose, and how long before refreshing slumber comes to your relief. Worry acts in a similar manner and we have all felt its disquieting influence, lying awake hour after hour in a vain attempt to calm the restless ac-



tivity of our thoughts. There is an irritability of the nervous tissue which is the product of exhaustion and an evidence of its defective nutrition, or what is equivalent, of its overstimulation. This irritability simply means weakened inhibition, which is as surely a sign of exhaustion as is the want of the power to react to an impression. Repetition of this prolonged hyperaemia leads to its easier production. The nutrition of the cells soon becomes permanently modified. They energize differently. The vessel walls become permanently distended. They are not equally strong at all points and aneurismal dilations or pouches form along their course. Obstruction results to the blood current. Nutrition is more greatly impaired. The contents of the vessels transude through their walls under the increased pressure and block up the peri-vascular lymph spaces. The changes in the vessel walls also favor this. The flow of the waste products is obstructed and the cells become bathed in the products of their own metabolism. The toxic effect of these still further deranges their functional activity. Permanent degeneration of the cells soon ensues. They change in form, their prolongations become rounded off, their interior becomes granular, or is filled with fat globules. The delicate plexus from which springs the afferent nerve fibrils is permanently damaged. The scavenger cells become enlarged, more visible and filled with the products of cell degeneration. Finally the entire cell is removed or so disorganized that its distinctive features entirely disappears. These changes are seen in exaggerated degree in such forms of mental disorders as parietic dementia, in which the nutritive changes and consequent loss of power are rapid and marked.

Bear in mind that in all these cases the incipient change, the first step in the degenerative process, is a simple error in cell nutritive, an interference with the opportunity to secure sufficient nourishment and a demand for more energy than the supply given will produce. When the problem is in its simplest form its solution should be comparatively easy, let it become complex through the lapse of time and its solution is no longer possible. when the vessel walls become changed in character or even dilated permanently, the recuperation is slow and does not always advance with the improvement in the general condition

of the patient. The nutritive error in the cell elements of the brain often continues long after the general condition has improved. I know of no other form of disease in which such patient perseverance in well doing is necessary.

The treatment of such nutritional errors is a complex subject. It will require every resource of the physician and tax his ingenuity to the utmost. It is by no means restricted to the use of medicinal agents. The first requisite is a sufficient supply of assimilative material of good quality as represented in healthy blood. The second is to secure the opportunity of the brain cells to receive this by a correction of the hyperaemia, obstruction or degeneration which has prevented it reaching them. The third is to diminish the demands upon the cells so that their work shall not be in excess of their recuperative power. The fourth is to secure the prompt removal of their waste products by clearing the channel of the lymph spaces of the debris which has come from the obstruction of the blood current. The fifth is to divert the functional activity of the cells from the directions in which it is defective, and to develop new functional tendencies, new habits of action, if such they may be called, to the end that the healthy balance may be re-established. We are required to repair their diminished inhibitory control and to stimulate them to activity where disuse has led to disorder.

We have not space to go further into details, but it may be said, in general terms, that medicinal agents are not so potent as the regulation of functional activity in the cell elements.

## NERVE HYGIENE.<sup>1</sup>

BY DR. AUGUSTUS FOREL.

Professor of Psychiatry in Zurich.

"Too many nerves and too little nerve," complains Professor von Krafft-Ebing of our generation. What do they mean, "nerves," "nervous," "nervous prostration," *neurasthenia*, and similar terms?

We must first clear away a common mistake, as if all this had reference to the nerves of the skin or of various parts of the body. It is no more these that are "nervous" than the fingers of an amputated arm which cause the pain that the former possessor of the arm imagines he feels there. Arm and fingers disappeared long ago, were buried after amputation and are now decayed, and yet there is a sensation of pain as if they were still present, the seat of the disease.

It is nothing but the brain that is "nervous." We make the mistake of attributing its excitement to the so-called sensory nerves of the body, because usually they convey to the brain the impressions of the external world, such as light, warmth, sensation of touch, sound and odors. It is the brain alone that occasions the sprawl, the convulsive twichings of the nervous woman, the deceptive senses of the victim of delirium tremens, the evil conduct of a drunken man, the great deeds of the genius, the indolence of the man who hangs around the saloon, the folly and the pain of insanity, the misdeeds of the criminal and the industry of the sober laborer.

In health, in the sound working capacity of the brain, lies the chief condition for happiness. Professor Hiltz is certainly right who believes that the happiness of an individual depends

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1. No apology is necessary for reproducing, in connection with the thoughtful article by Dr. Richardson, whose eminence as an alienist will command attention for what he writes, the above selection from the pen of one of the greatest psychiatrists of Europe. The subject, which is awakening remarkable interest on the continent, has hardly yet attracted merited attention here. Our obligations are to Mary G. Stuckenberg, whose translation (with slight modification) we borrow.

upon his fulfilling the purpose of his life by labor. But since man's labor is not accomplished like that of the plant and the lowest worm, for he applies a higher understanding and feeling to it, the fundamental possibility of happiness for him lies in a sound brain.

How are you going to convert a sound brain into a happy spirit, disposition and will, and keep them up? By continually patching at an impaired organ with medicines and cures in nerve or lunatic asylums? Such patchwork is good, or perhaps a necessity, if injury has already taken place, or has become great. But always the best prescription is prevention, in general, that one which any reasonable person can apply without either physician or apothecary.

Would you, by means of poisonous stimulants, urge the incapable modern brain to some unusual activity, which necessarily must exhaust and incapacitate still more? That would be putting out a fire with petroleum. Yet it is just what we are doing when we use alcoholic drinks, morphine and similar so-called nerve tonics. We injure the organ we desire to strengthen and wear it out prematurely. We see the fruits of alcohol-drinking in the saloon and in large part in the nervousness of our age. We see them in the prisons, the lunatic asylums, the idiots, the vagabonds, the idlers—consequences that are only partly the result of the drinking customs of these people themselves, those of their forefathers bear part of the blame.

Of course the use of alcohol is not the only occasion of the "nervousness" of our age. There are others, such as poverty, over-population of the cities, insufficient nourishment, but especially the unsuitable, the thoughtless marriages of stupid, eccentric or evil people, whose defective brain peculiarities perpetuate themselves in their posterity and contaminate society with incapable, lazy, untruthful, immorally inclined, in brief, with individuals that are a menace to the general good.

How ought and can we oppose these evils, successfully overcome our nervousness, and grow happier? That riches cannot make us either healthy or happy, that poverty occasions unhappiness and disease, has been so clearly shown that we need lose no words upon this subject. It stands approved by experience that nerves and muscles which remain inactive lose

strength and shrink; and just so the brain needs exercise, and in fact, earnest, hard labor, but not too one-sided, in order to become and remain strong and healthy. Over-weariness and over-exertion, however, injure the brain as they injure muscles and nerves. To furnish power and working capacity, the muscles and nerves require a sufficient amount of such nourishment as will produce matter and force; but over-feeding is an injury. It is just so with the brain.

Sleep is the indispensable rest of the brain during which it recovers the substance lost by the wear of the day and gathers up strength. Good sleep is the fundamental requirement for brain health. Every nerve stimulant, and on the other hand all substances that produce artificial sleep, are nerve poisons and are to be condemned by a healthy nerve hygiene. The worst foes of the human brain are alcohol, morphia, ether, cocaine, and the like. Their use is never justified except very temporarily as medicine, or in order to allay the pain and the agony of death in a fatal illness.

Every one who desires to secure and to strengthen a healthy and useful brain, must really labor, and that daily, and not too little. Four hours of work a day for a healthy being is altogether too little. Let any one spend his time in enjoyment and idleness, and enjoyment soon ceases to be enjoyment. He will accumulate artificial wants in ever increasing numbers until they burden his life. He will become more and more dependent and morose. His mental horizon will grow narrower continually and more rigid. The plastic brain of youth, that is, its docility and adaptability, will become less and less active and capable of comprehending and elaborating new thoughts.

On the other hand, mental labor preserves the plasticity of the brain to a much more advanced age. Idlers, therefore, in spite of the best brain capacity, become prematurely old mentally, narrow-hearted, limited in horizon, and not seldom absolutely stupid. We often observe moderately gifted students becoming, by means of work, men of power, and highly gifted young men, as a result of idleness, gradually grow useless, peevish, and now and then narrow-minded Philistines.

Secondly, one must not overwork. The work day must



not be prolonged into the night. One ought not to continue to labor with an exhausted, harrassed mind.

Thirdly, it is necessary to take sufficient nourishment, but one must not overeat—must partake of farinaceous food, the fats and albumen in proper proportions

Fourthly, eight hours of sleep are a necessity, and above all one must not retire too late. There must be no excesses of any kind.

Fifthly, all alcoholic drinks as well as all artificial producers of sleep and nerve stimulants must be absolutely avoided, as a matter of principle. Resolutely and bravely turn the back upon all places of tippling and seek the society of total abstainers, for to them belongs the future. Those people who wholly abstain from alcohol and the other things mentioned are more capable of work, healthier, happier and live longer. They do not endanger their posterity, run no risk of picking up some venereal disease in a state of intoxication. \* \* \* Poverty and social enslavement are also the daughters of alcohol and the mothers of nervousness and of brain stupefaction.

But nervous people and those who have weak nerves ought especially to regulate their lives according to these principles. Often they are cured by this means alone, without a physician, without drugs. Of course, however, since in their case the brain is already enfeebled, they are in need of a different prescription; they will be obliged to engage very moderately in mental labor, in fact, not at all until there is improvement, meanwhile exercising the muscles in order indirectly to provide the brain with power substance. The best means of all is ordinary labor on a farm, on generous, nourishing diet, and water. This method of cure I have prescribed for distinguished patients, ladies as well as gentlemen, which met with the very best success.

But thus far we have as yet done nothing to invigorate and improve the brain of our posterity. To take thought for that is certainly beautiful and important, although most people are too crass, egotistic or thoughtless to take practical interest. But in many cases only ignorance is the cause of criminal neglect of the subject. It is to the latter we address ourselves.

It is criminal towards posterity to bring forth children

thoughtlessly or without taking counsel with conscience. The tendency to crime is transmitted, stupidity is transmitted, mental aberration is transmitted, malice is transmitted, indolence is transmitted, selfishness is transmitted; but, on the other hand goodness is hereditary, industry is hereditary, mental and physical health are hereditary, conscience and disposition are hereditary, intelligence is hereditary. Training and the experiences of life may more or less develop or arrest the hereditary disposition, but they can never produce or destroy them. Alcohol destroys the gifts of nature in the embryo of the brain, injures all of them and never can improve one iota.

When the love of a man and a woman for each other awakes a desire to become united for life, they ought never to forget that they are undertaking a very grave responsibility, the responsibility for their future children. They ought to renounce marriage rather than to produce physical, or what is much worse, mental cripples. Unfortunately, however, we see noble people with highly gifted natures who carry their prudence to so anxious an extreme as not to marry, or at least not to bring forth offspring, while the most frivolous, brutal and stupid, under the protection of lax laws that had their origin in a mistaken humanity, multiply like rabbits and carelessly abandon their progeny to the state or to public philanthropy—progeny made more liable to danger by reason of previous alcoholic excesses.

And with such false political economy, such mistaken breeding, is it any wonder this increase in the number of mentally diseased, of lunatic asylums, of a weak-eyed proletariat, of morally defective vagabonds and criminals? There is talk of overwork as the occasion of these evils, overlooking the fact that this proletariat mentally never has overworked, but rather has been indolent and useless always. "Nervousness," really brought about by means of mental overwork, forms only a small and comparatively safe fraction, while the great, innumerable company of mental wrecks nearly always owe their catastrophe to diseased or defective brain conditions, to excesses, and in enormous percentage, to alcohol.

It is therefore a duty to consider hereditary conditions. Every respectable woman ought to look for solidity, soberness,

good sense and a good disposition, as she chooses a bridegroom. The capable young man ought to have a care not to marry a money-bag, or a hysterical siren, or a body without a soul, but a sensible, modest, industrious, respectable and intelligent young woman.

Meanwhile, let the able-bodied and sound of brain not be affected by any silly, pessimistic philosophy, but seek each other in love and in marriage, bring forth children without careful regard of money, for, with the right choice in marriage, good fortune will not fail them.

But what shall we do with the others, with the eccentric, stupid, wicked, defective? This is a question as difficult as it is critical. They should be prevented from multiplying themselves, for they will only bring forth mental cripples, unhappiness for themselves and for their children. They bring forth unfortunates who will afterwards execrate their parents. One simple and safe counsel that ought, however, to reach the good as well as the evil, the highest genius as well as the dullard, would prevent much evil. Renounce forever all those systematically stupefying, brutalizing and demoralizing factors of human misery—the alcoholic drinks, and also the so-called “enjoyment” of narcotics. Flee the perilous counsel of the pessimists, who cry: “After us the deluge.” That flood of mental disaster which these very people, so heartless and selfish, inflict upon their descendants may overtake themselves before death reaches them; for selfishness brings forth misery; love, happiness.

## LOCALIZATION IN THE CAT.

BY C. L. HERRICK.

An operation, performed in connection with Mr. E. G. Stanley, which it is hoped to describe in full in a subsequent issue, perhaps deserves notice on account of its suggestiveness upon points raised in Munk's last paper in the Proceedings of the Berlin Academy.<sup>1</sup>

Munk states that in the dog and monkey the region for the extremities is concerned with the formation of tactile and pressure sensations and perceptions of the limbs of the opposite side. The tactile reflex is also located in this region and is completely lost when it is extirpated. In addition to this, this region is at least chiefly responsible for the pain sensations of the members; pain is dependent for its perception up to a certain degree of intensity on this region, and complete extirpation of the region nearly destroys the sense of pain which may gradually be gained by substitution of other regions. Again, there is a connection between the cortical centre and the reflex centre for the limbs, and that which inhibits the reflexes.

After removal of these areas the animal moves awkwardly, lifting the feet too high or too little, placing them irregularly so that the feet double under. There is a tendency for the feet to slip laterally from the body permitting the body to fall toward the side opposite the operation. These irregularities disappear, so far as superficial observation goes, completely.

The feet corresponding to the operation lose their responsiveness to slight tactile irritation. When a strong pressure is brought to bear there is reflex response, *i. e.* movement of the limb, but no evidence of sensation, as is proven by the fact that the head is not turned toward the irritated member as it is toward any other.

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1. Ueber die Fehlsphären der Grosshirnrinde. Mittheilungen aus den Sitzungsber. d. Königl. Preuss. Akad. der Wissenschaften zu Berlin. July, 1892.

Bechterew's mistake, according to Munk, is in not removing the entire region, enough of the cortex remaining to explain the evidence of sensation brought forward by the former.

Munk distinguishes between tactile reflex and general reflex. The former is completely lost, the latter reduced, but subsequently regained. He seeks to explain a part of the phenomena supposed by Goltz to be due to the repressive effect of irritative processes as the result of isolation.

Our subject was a half-grown kitten, and portions were removed from the left hemisphere in three successive operations, so that a long, narrow area extending from the crucial sulcus to the limits of the middle external gyrus caudad, and including nearly the whole of that gyrus, was extirpated. The entire thickness of the cortex and most of the white matter was removed. The first operation was apparently near the front of Munk's visual sphere and the kitten showed some disturbance of vision in the opposite eye, but, though the incision was subsequently carried further caudad, these symptoms did not reappear. After the last operation, which invaded the fore-leg area of Munk, there was decided disturbance of the motor and sensory functions for both limbs. The skin sensation and reaction against pain was reduced immediately after the operation, but these disturbances soon disappeared. The voluntary motion was but little disturbed but the fore foot tended constantly to double under and trip up and slipped helplessly away from the line of support. The hind leg was similarly affected, sliding laterad and failing to support the body. In walking and running no imperfection was noticeable, except when obstacles or changes in the direction of motion called out what has been described. Most noticeable of all was the change in the position of the limb when permitted to hang free. If the body were supported upon the ventral aspect the left legs were drawn up and quickly responded to any tendency to fall in that direction, while the right legs hung pendant and failed to react against a push threatening a fall to the right. The kitten was watched four or five weeks, during which time nearly all symptoms disappeared except those last mentioned, which remained to a certain extent to the last. Another curious effect of the operation was a strong tendency, for some time after the extirpation, to shake the feet of the right side (rarely



the left hind foot in sympathy), as if they were wet or otherwise irritated. The shaking was apparently a reflex and was at times almost convulsively violent. It is to be compared with the scratching reflex described by Goltz.

In contradistinction to Munk, therefore, we find loss of muscular sense a more important and permanent feature than tactile or pressure disturbance, though the extirpated area extended further caudad than in his experiments. It must be observed that the area we removed lies farther from the median line than that operated on by Munk and affected directly only his fore limb area, though the depth of the excised portion suggests the possibility of an injury of other tracts.

We are confident, moreover, that many of the contradictory results of experiment are due to proliferating regenerations which supply the lost material in the case of young animals.

#### A SIMPLE ALCOHOL FORMULA.

Students frequently experience difficulty in recalling the proportions in which water should be added to alcohol of various grades to prepare the stock solutions for hardening gradatim. The formula given in our guides are singularly and absurdly complicated. The following may be suggested: Take as many parts of the alcohol given as the percentage required; add as many parts of water as the difference between the given and the required percentages.

*Example.* Given 70 per cent. alcohol to make 40 per cent. Take 40 parts alcohol of 70 per cent. and  $(70-40)$  30 parts water.

## LITERARY NOTICES.

### HISTOGENESIS AND COMBINATION OF NERVOUS ELEMENTS.<sup>(1)</sup>

At the time of its separation, the medullary plate consists of a single-layered epithelium. The cells soon begin to vary, some enlarging at the peripheral portion and others entad. The nuclei in each case move toward the larger end of the cell and thus form two or more rows, though remaining nearer the middle than the ends of the cells.

The body of the cells soon differentiates into a transparent fluid or gelatinous substance and a more dense granular or striated portion. Usually the first step in this differentiation is the formation of vacuoles which, as they increase in size, tend to coalesce.

The denser reticular portion accumulates in the peripheral portion of the cells. Thus, briefly stated, the original epithelium cells form a frame-work, which His calls the myelo- or neuro-spongium, the individual cells being spongioblasts. The nucleated bodies of the spongioblasts form a broad *median zone*, while the outer and inner margins are devoid of cells. The inner or *columnar zone* consists of longitudinally striate columns, which expand at the inner surface to form a continuous *marginal layer*. The outer marginal or *mantle zone* (*randschleier*) consists of a reticulum of fibres which is penetrated by radiating pillars expanding at the periphery.

The nervous elements appear at an early stage in spaces between the ventricular part of the epithelium cells in the form of germinal cells of uncertain origin. The number varies with the stage of development, being especially abundant at the time of the appearance of the first nerve roots. The period of maximum development also varies with the locality, being earlier in the cervical than the cerebral or lumbar regions. The number diminishes gradually and this reduction takes place earlier in the ventral than the dorsal half of the medullary plate.

These germinal cells at a definite time begin to change their form, becoming acute peripherally, until they give rise to a more or less thread-like process, which becomes the nerve fibre, connected at its base

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<sup>1</sup> WM. HIS. Histogenese und Zusammenhang der Nerven-elemente. Referat in der anatomischen Section des internationalen medicinischen Congresses zu Berlin. Sitzung von 7 August, 1890. Archiv. f. Anat. u. Phys., 1890. Supplement-Band. p. 95.

by a conical cap of protoplasm with the nucleus of the cell or neuroblast.

During the period of transition when the germinal cells are being transformed into neuroblasts, they are motile. In the first place, they move ectad between the cells of the columnar zone, but find a hindrance to their farther migration in the mantle zone. Along this contact line the neuroblasts assemble, forming a mantle layer, of which the dorsal and ventral portions react dissimilarly. The cells of the dorsal half, because of the oblique position of the epithelial frame-work, strike the mantle zone at an angle and turn parallel to the surface. Their fibres describe long curves ventrad and, in part, reach the median line.

The cells of the ventral region on the other hand impinge more or less perpendicularly upon the mantle layer and, though the cells do not penetrate it but collect in clusters, the fibres make their way through this zone and pass out as motor nerve fibres.

The migration of neuroblasts is especially extensive in the medulla. The thick lateral walls of the tube here are divided by a groove into a dorsal plate or ala and a ventral half or basal plate. In the latter the groups of neuroblasts form the motor niduli of the hypoglossus, accessory, vagus, and glossopharyngeal. On the lateral margin between the ala and basal plates lies the *tractus solitarius* containing the sensory fibres from the vagus and glossopharyngeus. The margins of the alæ fold outward and the two lips of the fold grow together. From this evaginated portion there arise multitudes of neuroblasts which pass medianly entad from the *tractus solitarius* to near the median line. Out of the clusters thus derived arise the olives and accessory olives, the fibres from which cross the median line within the raphe. Blood vessels enter the walls of the medullary tube at an early period but it is not until a much later period that ameboid cells transude into the neuroglia and lodge in its meshes. These connective or wandering cells constitute the third element of the complex.

The neuroblasts of the medullary plate produce intramedullary fibres as well as motor nerve roots. The sensory roots spring from the spinal ganglia, the cells of which assume a bipolar form and extend into two fibres, one passing centrad, the other peripherad. The central processes collect at first upon the exterior of the medullary tube in special longitudinal fasciculi which, in the cord, form the primary posterior fasciculus, and in the brain constitute the ascending roots (as the ascending root of the trigeminus and the tractus solitarius, or common ascending root of the glossopharyngeal and vagus).

The origin of the spinal ganglia, though long controverted, is doubtless from that portion of the ectoderm connecting the medullary plate with the definitive ectoderm where a groove-like depression with numerous germinative cells forms as the medullary tube separates. These cells are originally motile and multiply by division until they reach their ultimate site.

The sympathetic ganglia arise much later than the spinal (at the beginning of the second month in man). The thick stem of a spinal nerve divides where it comes in contact with the dorsal margin of the cœlom, giving off a visceral branch, some fibres of which reach the aorta, while others turn longitudinally, there being no sympathetic cord or ganglia at this stage. Onody<sup>(1)</sup> considers that the sympathetic ganglion originates as an outgrowth from the ventral portion of the spinal ganglia. He believes that undifferentiated motile elements wander out of the spinal ganglia and transform themselves into sympathetic ganglion cells. The lateral sympathetic ganglia are, in their turn, points of origin for the visceral ganglia.<sup>(2)</sup>

His has shown in earlier papers that the olfactory grows from an external ganglion into the brain as do other sensory nerves. The olfactory ganglion adheres secondarily to the olfactory bulb. In all probability, its cells are derived from the epithelium of the olfactory region of the nasal cavity.

The origin of the eighth fibres is to be sought in the bipolar ganglion cells of the ganglia vestibuli and cochleæ, and of gustatory fibres in the ganglion cells of the glossopharyngeus.

In the case of the optic nerve the relations are more complicated. From the investigations of Ramon y Cajal it appears that its stalk contains fibres springing from the central as well as the peripheral region.

The neuroblasts of the retina spring from germinative cells which develop near the ventricular surface. The granular layer corresponds to the mantle zone of the medullary plate.

It appears, therefore, that in the development of the nervous system and sensory organs two forms of cells are differentiated at a very early period—the germinative and epithelial cells. One furnishes the specific elements, the other the frame-work.

In general, every nerve fibre springs from a single cell. Until the recent observations of Golgi it was supposed that the nervous process of a cell was always unbranched, but Golgi has shown that not only is the axis cylinder provided with processes, but in cells of the second type the axis cylinder divides into a complete mesh-work. Thus the distinction between axis cylinder and other processes of the cell disappears. Yet embryology shows that the former is very distinct from all others in being the first, and for a long time, the only process. The nerve cells develop much later in the brain than in the cord.

The nervous processes continue to grow perhaps for months, and when the blunt end reaches its ultimate terminus it usually divides dichotomously into a cluster of fibrils. In Pacini's and Krause's corpuscles we have instances where, instead of dividing, the terminus forms an endothelial capsule with soft contents. In another form of end organ,

<sup>1</sup> Cf. A. M. PATERSON. On the Development of the Sympathetic System. *Philos. Trans.*, 1890, A. p. 159, as reviewed elsewhere in this number.

<sup>2</sup> *Arch. f. Anat. u. Entwickl.*, 1885.

Graudry's body, the nerve forms a flat disc-like plate. Those fibres which extend to the epidermis pass to the epithelium and subdivide, forming fine fibres lying free in intercellular spaces. In muscles the nerve fibres penetrate the substance and end in the branching muscle plate. In unstriped fibres the nerve fibres are said to extend to their nuclei, while the connection between sensory nerve and specific cell seems to be a sort of splicing by intimate contact not involving actual continuity.

In respect to the fibres entering the central organ, the first clue was given by the discovery of Cajal that the optic nerve fibres arising in the retina terminate freely in the quadrigemina in the form of much branched tufts. The sensory fibres entering the cord divide into an ascending and descending branch, each of which sends collateral off-shoots into the gray matter of the two cornua, where they generally embrace a nerve cell in a mesh-work without uniting with its processes.

Cajal and Koelliker have shown that the protoplasmic processes of medullated nerve fibres do not anastomose, but end in free stumps. Instead of the earlier notion of a nerve reticulum that of a neuropileum is suggested. The gray substance contains in the meshes of its reticulum innumerable termini of nerve fibres and protoplasmic processes, which are imbedded in a diffuse stroma which must constitute the means of communication. The reaction will necessarily pursue the path of least resistance.

#### THE NERVOUS SYSTEM OF THE GORILLA.<sup>(1)</sup>

This beautiful quarto volume of 78 pages, with heliotype plates of the nervous and vascular systems, is an important addition to the rather meager anatomical data upon anthropoids. The following summary may serve to indicate the differences between the peripheral nervous system of the gorilla and of man, as well as to afford a basis for other comparisons.

1. The *facialis* of the gorilla is more complicated than that of the chimpanzee, but less so than that of the orang or of man.

2. The *glossopharyngeus* of the left side forms a plexiform reticulum and gives off anastomosing fibres to the vagus and sympathetic, forming nearly all the rami pharyngei. On the right side it anastomoses with the hypoglossus and conveys to it fibres of the vagus and sympathetic.

3. The *vagus* sends a depressor branch to the cardiac plexus from either side. The internal branch of the right superior laryngeal is divided, the upper part passing through the membrana thyrohyoidea, the lower, in connection with the external branch, through a foramen in the cartilage. The cardiac branch of the right side passes

1. EISLER, PAUL. Das Gefäss und periphere Nervensystem des Gorilla. Nine plates. Halle a. S. Tausche und Grosse, 1890.



through a trachealis plexus, but the left cardiac passes directly to the heart.

4. The descending rami of the *hypoglossus* contribute to the innervation of the sterno-cleidomastoides muscle, while the ansa hypoglossi are supplied solely from the first two cervicals.

5. The *auricularis magnus* and *subcutaneus colli medius* arise only from C. II, the *suprascapulares* from C. II-IV.

6. The *phrenic* nerve of both sides contains indubitable sympathetic fibres, and on the right it is directly connected with D. I and the ganglion stellatum.

7. C. VII on the right side for the most part and on the left entirely passes to the middle medianus root of the brachial plexus.

8. The *suprascapularis* arises from C. IV and V, instead of C. V and VI, as in man.

9. The *dorsalis scapulae* is present only partially on the left side, being replaced by C. III and IV (and for the M. rhomboides by D. III and VI).

10. The *axillaris* springs from all the plexal nerves and contains also the branch to the teres major.

11. There is no distinct *subclavius*.

12. *Cutaneus brachii internus* is chiefly formed from a lateral branch of D. I and the inter-costo-humeralis.

13. The *musculocutaneus* receives no fibres from C. VII and gives off a branch to the coracobrachialis muscle.

14. The *ulnaris* and *medianus* give a fine fibre to the brachialis artery. The ramus volaris profundus of the unar springs from a strong anastomosis with the medianus, passing under the lig. carp. volare into the hand.

15. The *cutaneus brachii post. sup.* of the radialis is wanting, its place being taken by a descending branch of the axillaris.

16. The *clunium superior* and a subcostalis passes from D. XII under the thirteenth rib.

17. The *ileoahypogastricus* receives a branch from D. XII.

18. The *genitocruralis* bears fibres for the rami communicantes of the sympathetic and the obturatorius.

19. The *cruralis* receives most of its fibres from L. IV.

20. The *peroneus* springs from the posterior surface of the ischiatic plexus, as also the clunium inferior, glutei, and pyriform nerves, while the tibialis, cutaneus fem. post. and the nerves to the obturator internus quadratus gemelli and flexors cruras spring from the anterior surface.

21. No fibres caudad to the second sacral enter the ischiatic plexus.

22. The pudendalis plexus is formed by the second and third sacrals, while coccygeus plexus springs from S. IV and V.

23. The *tibialis* and *peroneus* each give off to the knee an articular branch with numerous Pacini's bodies.

24. The *peroneus profundus* supplies the adjacent sides of the second and third toes.

25. The *plantares lateralis* and *medialis* anastomose within the adductor obliquus halucis, which both supply.

26. The flexor digitorum brevis is innervated from the *plantaris lateralis*.

27. Three isolated cervical sympathetic ganglia besides the stellatum are present.

28. The *ganglion meseraicum medium*, which is wanting in man, lies between the celiac plexus and the aorticus. Especial emphasis is laid upon the great distinctness of parts in the lumbosacral plexus. The analysis of this plexus has proven impossible in man, but in the present case the several nerves may each be followed to the plexus, excluding any doubt as to their origin. In this, as in the brachial plexus, a ventral and dorsal portion may be distinguished. Thus a distinct advance is made in settling the homologies of the limbs. In general only related nerves can substitute for each other in the innervation of a given group of muscles. Ventral muscles can only be supplied by ventral branches of spinal nerves and vice versa.

#### THE ORIGIN AND CENTRAL COURSE OF THE EIGHTH NERVE.<sup>(1)</sup>

These observations are based on the study of sections stained by Weigert's method after destruction of the auditory organs from the cervical aspect. In cases where the cochlea alone was injured there was atrophy of the posterior root of the eighth, the anterior nidulus of the acusticus and the tuberculum laterale. There was also a reduction in the number of fibres in the corpus trapezoides and the upper olives. Farther cephalad there was evidence of degeneration in the ventral fillet of the opposite side, which could be traced as far as the arm of the testes. The striæ medullares were somewhat atrophied, enabling Baginsky to trace their course as follows: Passing from the tuberculum laterale of the medulla and in part from the anterior acusticus nidulus they pass ectad to the restiforme, crossing dorsally to the median side and there divide into two bundles, both of which pass to the upper olives, though a few fibres enter the arcuate bundles. The decussation is complete in the corpus trapezoides, as stated by Fleschsig. Serious operative difficulties stand in the way of the destruction of the anterior branch of the eighth and in the experiments cited only partial success was secured. The fibres from the anterior root lie upon the median surface of the restiforme. Farther cephalad there appears another bundle lying ventrad which arches ventrad, to be lost in the formatio reticularis. Still a third tract from the same root radiates from the ventral aspect of

<sup>1</sup> Ueber den Ursprung und den centralen Verlauf des Nervus acusticus des Kaninchens und der Katze. B. BAGINSKY. Math. u. naturwiss. Mith., Berlin, Akad. 1889, VI., pp. 441-445.

the restiforme toward the walls of the fourth ventricle. The cells of this region were in part atrophied.

A certain amount of atrophy appeared in the inner part of the crus of the cerebellum, which did not however extend above one-third the length of the anterior root of the eighth. Deiter's nidulus sustains no relationship to the acusticus.

#### THE DEVELOPMENT OF THE SYMPATHETIC SYSTEM.<sup>(1)</sup>

The cells of the ganglia of the sympathetic chain are shown by Gaskell to be trophic simply. The gray *rami communicantes* spring from the ganglia and are distributed as trophic fibres to the roots of each spinal nerve and their meninges and the bodies of the vertebræ. The white *rami communicantes* are only between the tenth and twenty-fifth spinal nerves and in the rami of the second and third sacral nerves (in the dog).

In the anterior region the white rami pass from the spinal nerves to the ganglia and there separate into two groups; one set forms vaso-motor fibres which are distributed peripherally as gray fibres, the other set does not join the ganglia, but forms visceroinhibitory fibres in the abdomen. The white rami of the posterior region pass to the hypogastric plexus without joining the ganglia and form *nervi erigentes* (vasoinhibitory) and perhaps visceroinhibitory fibres.

Patterson believes with Gaskell that the sympathetic is primarily unsegmented. Two views prevail as to its origin. Onodi and Birdsell consider it a distinct proliferation from the spinal ganglion, and Balfour from the spinal nerve (in either case ectodermal).

In mouse and rat embryos of about eight days the first indication of the formation of the sympathetic cord has been found. The general condition of development then corresponds to that of the chick at the end of the third day. The spinal nerve has extended almost as far as the somato-splanchnic angle, and to the cardinal vein in places where the latter is present; and in some sections the superior primary division is visible. A change is now apparent among the cells of the mesoblast surrounding the aorta. In the interval between the latter and the cardinal vein an irregular group of cells is seen on the ventral side of the intercostal arteries. This mass is composed of cells which stain more deeply; the nuclei are larger and they are more often multinucleate than adjacent cells.

The mass is comparatively large cephalad, and tapers off and becomes indistinct caudad. There is no connection, fibrous or cellular, with the spinal nerves or ganglia. Longitudinal sections show that this mass is a long rod or column on either side the median line, consisting of fusiform cells with ovoid nuclei and thread-like processes.

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1 A. M. PATTERSON. Development of the Sympathetic System in Mammals, Philosoph. Trans. Roy. Soc., Lond., 1890, pp. 159-186, 9 plates.

The column can be traced as far as the level of the mouth and caudad as far as the Wolfian bodies, where it becomes connected with a mass of mesoderm cells which form one portion of the supra-renal bodies. This rod is mesodermal in origin; it is formed *in situ*, and it is unsegmented and unconnected with the spinal nerves.

In rat embryos at about ten days cellular outgrowths from the cellular sympathetic cord can be traced ventrally round the aorta, especially in the region of the kidney, and in front of it to form the collateral ganglia, and to join the supra-renal bodies.

The superior (dorsal) primary division of the spinal nerve is not yet differentiated into separate roots. The somatic part of the inferior, (ventral) primary division has divided into its dorsal and ventral branches. The splanchnic part is directed inwards above the cardinal vein and reaches nearly to the sympathetic cord.

In mouse sections at eleven days the union between the splanchnic branch and the sympathetic is complete.

In front of the fore limbs and behind the kidney no such connection of the splanchnic branch with the sympathetic can be made out.

Up to the time of the formation of the vertebral centra there is no ganglilation or constriction of the main sympathetic cord.

The formation of ganglia is determined first, by the entrance of the splanchnic nerves; second, by the position of the cord with reference to the vertebral column.

The splanchnic branches correspond to the white *rami communicantes* and are derived from both the dorsal and ventral roots of the spinal cord.

The gray *rami communicantes* arise from the sympathetic cord as cellular outgrowths, which find their way along the splanchnic branches to their central connections.

#### THE EPIPHYSIS AND THE PARIETAL EYE.<sup>(1)</sup>

This discussion of the relation of the epiphysis to the so-called parietal eye is timely and fills an important gap in our knowledge. While anything like a complete construction of the facts presented must await embryological investigation of these types, yet the observations are suggestive.

Mr. Ritter describes the parietal vesicle in *Phrynosoma* as lying within the parietal foramen, though extending somewhat above the parietal bone and firmly imbedded in connective tissue. The various tissues above the parietal vesicle are all modified and the skin is unpigmented. A cord of connective tissue passes from the end of the epiphysis to the sheath of the vesicle, but no evidence could be secured of their actual passage through the walls. The wall of the vesicle

<sup>1</sup> W. E. RITTER. The Parietal Eye in some Lizards from the Western United States. *Bulletin of the Museum of Comparative Zoology*, Jan., 1891.

is distinctly differentiated into lense and retinal portions, the line of demarkation between them being distinct.

The epiphysis consists of a curved cylinder of a composite character, the greater portion consisting of plexiform epithelium. Distally connected with the plexus is a vesicle which is composed of columnar and, in some species, pigmented epithelium. The cavity of the vesicle is stated not to be connected with infundibuliform proximal portion of the epiphysis. Connective fibres pass from the vesicle to the parietal organ. An immense blood sinus covers the epiphysis on the caudo-dorsad aspect.

Ritter concludes that the parietal organ is a degenerate eye, though having no nervous connection with the brain. He thinks, however, that the epiphysis may have secondarily acquired some function in connection with the lymph system.

A very complete bibliography adds value to the paper.

#### BRAINS OF DINOSAURS.<sup>(1)</sup>

Two points in the paper quoted are of interest to neurologists; first, the new evidence as to the former functional condition of the pineal eye, and second, the primitive condition of the brain.

At the union of the squamosal and parietal bones there is a median foramen which Marsh calls the "pineal foramen." It is the same as the opening termed parietal foramen by other writers. "In old individuals it is nearly or quite closed. When open it leads into a large sinus, extending above the brain case into the cavities of the horn-cores. This foramen has not before been observed in Dinosaurs."

"The brain of *Triceratops* appears to have been smaller in proportion to the entire skull than in any known vertebrate. The position of the brain in the skull does not correspond to the axis of the latter, the front being elevated at an angle of about thirty degrees. The brain-case is well ossified in front, and in old animals there is a strong septum separating the olfactory lobes."

Even when compared with *stegosaurus* the brain seems of a low type. The hemispheres are practically absent. An enormous fossa for the reception of the hypophysis and a great development of the optic, trigeminal and other cranial nerves are characteristics shown by the casts.

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## LITERARY NOTICES.

### THE TROPHIC FUNCTION OF NERVES.

It is to be feared that teachers and investigators are prone to greatly underestimate or ignore those functions of centrifugal nerves which fail to express themselves in actual muscular contraction. Such acts as perspiration, weeping and congestion are obviously under the control of the nerves, and as long ago as 1854 Virchow claimed that fever is an expression of nervous activity. In addition to such temporary effects of the nervous system on the vegetative, more permanent changes may be noted, embracing atrophy, hypertrophy and hyperplasy, consisting in the diminution or increase in organs through nervous influence. Paraplasia, or the production of new structures from old ones, also occurs in various forms as the result of neuropathies.

The amount of influence exerted upon organs remote from nerve centres and indirectly connected with them, both as regards function and growth in abnormal conditions of the nervous mechanism, is suggestive of the great influence of the nervous system upon the development, correlation, and growth of the same organs under normal conditions. From a most suggestive article by Professor Arndt on this subject most of the following notes are compiled.<sup>(1)</sup>

It has long been recognized that the section of the trigeminal and vagus nerves produce pathological changes in the mucous membrane of the eye, nasal passages, mouth, and in the lungs. The fact that the sensory nerves supplying these organs are of necessity simultaneously cut has led to the suggestion that the irritation is due to external sources which would have been perceived and removed but for the loss of sensation.

That this assumption is incorrect is shown by a comparison of cases where gouty or rheumatic patients are prevented from the use of the limbs because of joint affection, the motor nerves themselves being relatively uninjured, with cases of paralysis due to central nervous disturbance. In the former case there is no special tendency to decubitis (a degeneration of the tissue in the extremities often accompanied by

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1 ARNDT, RUDOLF, "Ueber trophische Nerven," *Archiv f. Anat. und Physiol. Physiol. Abth.*, 1891, p. 54.

great pain), while in the latter an acute form of this affection may rapidly set in.

In cases where the ischiatic nerve has been cut, as in the guinea-pig for the purpose of inducing epilepsy, the limb is paralyzed and becomes inflamed, swollen and discolored. In a short time spontaneous sores appear, and the toes are lost, leaving a deformed stump, which, nevertheless, ultimately heals and remains well, evidently because of a restoration of nervous connections.

A case where all the soft parts of an arm had been accidentally cut and prevented from healing by first intention illustrates the same point. Only the A. interossea were uninjured, and decubitus resulted in a few days, followed by swelling of the fingers. The hypertrophy of the joints seems to have been persistent. This the author ascribes to the section of the nerves.

In the case of the guinea-pig before referred to, there develops on the neck on the same side as the injured leg a so-called epileptogene zone or area. In this region the skin becomes gradually more sensitive, until finally the hair falls out, and pinching the skin in this area gives rise to epileptiform symptoms. The disturbances in the skin bear an unmistakable resemblance to the accompanying changes in the leg.

These trophic disturbances certainly are not due to loss of sensation, but to reflex modification in the innervation.

In this connection the many cases may be noted where a great mental excitement (fear, anger, etc.) produced functional derangement of the visceral organs. A case referred to by the author exhibited not only liver-disturbance, but albuminuria and other kidney affection. The author suggests that the nervous excitement was so great as to actually destroy the epithelial cells of the kidney, which, accordingly, had an unusual shrivelled appearance.

Gouty people often afford illustrations of trophic disturbance resulting from nervous excitement. Gout itself is regarded as a neuropathy by the author. The following diseases may also result from neurotic causes: erythema, erysipelas, urticaria, herpes, prurigo, eczema, pemphigus, pityriasis, psoriasis, acne, furunculi and lupus.

The fact that weak and nervous people lose the hair or become gray upon bilaterally symmetrical areas of head and face points to a nervous origin of baldness, etc. The symmetrical degeneration of the body is but the converse of the law of symmetrical bilateral growth, and both are to be referred to the bilateral nervous control. Such control can only be explained by the assumption of nerves charged with the nutritive function, *i.e.*, trophic nerves. How, then, does it happen that trophic nerves have never been demonstrated anatomically? The author answers that it is because we have not been clear as to what was sought, that the real trophic nerves have long been known.

The nervous system, in this view, is rather an interdependent reflex complex in which every part exerts its influence than an automatic

centre with distributing tracts. As a result of each molecular disturbance, the end cells suffer a change in the processes of metabolism, which change will vary with the nature of the cells (tendon, muscle, etc.). The nutritive processes are there influenced through the more elementary metabolic processes. Every nerve, and especially every centrifugal nerve, is therefore a trophic nerve. The various processes governed by these nerves (secretion, contraction, etc.) are simply the results of the trophic influence.

For example, the young muscle cell contains an irregularly arranged mass of granules, which gradually arrange themselves into the transverse bars so characteristic of voluntary muscle. This structure is the result of the oft-repeated contraction. It has been observed that, in contraction, the elementary granules enlarge, and their combined increase causes the increase in diameter of the Bowman's discs or dark stripes. The author regards the only satisfactory explanation to be an increased absorption of fluid from the light portion of the fibre, which absorption is the result of altered molecular conditions or a form of metabolism brought about in the granules by the nerve stimulus. In a similar way the centripetal nerve gives rise to sensation simply because its stimulus alters the vital activity of its central terminal cell.

Thus there are no special trophic nerves because every nerve is trophic. The distinction between sensory and motor nerves, while useful for convenience sake, is more accurately expressed by centripetal and centrifugal.

#### DEGENERATION AND ATROPHY AS A RESULT OF SECTION OF THE CRANIAL NERVES.(<sup>1</sup>)

This exceedingly interesting paper affords a brief historical review of the development of the v. Gudden-Waller method of experiment. Mayser, Ganser, von Gudden and the author had been associated for a number of years in this difficult department, with results which certainly substantiate the author's claim for it. Two classes of experiments are chiefly relied upon:

1. A cell group is extirpated in a young animal. When adult the associated fibres are atrophied, enabling one to trace the course of the tract in question in detail. In this way, after injury to the Gasser's ganglion, the author demonstrated the loss of the fibre branches in the substantia gelatinosa of the tuberculum Rolandi, and Monakow found similar result in the corpus geniculatum externum after enucleation of the eye, while Gudden determined that the pyramid fibres pass directly into the cord by extirpation of motor areas.

2. A nerve root or fibre system is sectioned in a young animal, and,

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<sup>1</sup> FOREL, AUG., "Ueber das Verhältniss der experimentellen Atrophie und Degenerations-methode zur Anatomie und Histologie des Centralnervensystem," Festschrift zur Feier des fünfzig-jährigen Doctor-Jubiläums der Herren Prof. Dr. Karl Wilhelm von Nägeli und Prof. Dr. Albert von Kölliker, Zurich, 1891.

when mature, the corresponding niduli are found to be degenerated. In this way Gudden has identified the niduli of the nerves of the eye-muscles, Ganser discovered a degeneration of retinal elements after section of the optic tracts, Monakow demonstrated degeneration of the cortical pyramidal cells after section of the pyramidal fasciculi, and Mendel corrected Meynert's account of the acoustic.

The experiments described in the present paper were all by the second method, and related to the ninth, tenth and twelfth nerves. The section of one of the roots of the latter in the young causes entire loss of the nidulus, though without affecting the small-celled hypoglossus nidulus of Roller, and proves that there are no crossed fibres.

There is no connection with the olives, and the various parts of the true nidulus (Stilling's nidulus) are not connected with each other or the opposite side.

The author denies (somewhat inconsequently, we think) any connection with the nidulus of the lateral fasciculus, nidulus of the vagus, or dorsal longitudinal fasciculus.

Extreme difficulty attends experimentation upon the ninth and tenth and it is usually impossible to avoid injury to the eleventh. Mayser, however, succeeded in extirpating the ninth and tenth, and our author figures and describes the sections of one of these brains.

The definite results are the following:

1. The sensory fibres of the lateral mixed system (IX-XI) spring from the fascicularis solitaris or respiratory bundle and end between the cells of the surrounding gelatinosa.
2. The motor fibres of the vagus and glosso-pharyngeal spring from the nidulus cephalad and dorsad of the hypoglossus nidulus.
3. There is no decussation in either case.

#### THE DEVELOPMENT OF THE SPINAL GANGLIA IN MAN.

Lenhössek<sup>(1)</sup> has availed himself of the section of a human embryo 2.5 mm. long and possessing twenty myomeres to discuss anew the origin of the spinal ganglia. The results may be thus summarized. At an early period the material of the future ganglia separates in the form of an unsegmented band on either side of the medullary plate. It is distinguished by its spherical cells—ganglioblasts. The closing of the plate to form a tube brings the two bands toward each other, and results in a temporary union. Soon, however, a rapid proliferation of the cells results in a return to their lateral position and an indication of segmentation. The method described is similar, except in unimportant details, with that described in other groups by His and Beard. The author, however, believes that the medullary nerve plate includes the germs of the sympathetic system, as well as of the central and peripheral.

<sup>1</sup> LENHÖSSEK, M. v., "Die Entwicklung der Ganglienanlagen bei dem menschlichen Embryo," *Archiv f. Anat. und Phys.*, 1891, I.

## PERIPHERAL CONTROL OF THE CIRCULATION IN THE BRAIN.

An editorial in the *Alienist and Neurologist* for July, 1891, calls attention to a fact of much significance in physiology, aside from its value in neurotherapy.

M. Onimus<sup>(1)</sup> shows that the application of the continuous galvanic current to the sciatic nerve produces sleep. This is in accord with the well-known fact that stimulation of the sciatic produces changes in the cerebral circulation. The observations were made upon patients suffering with atrophy of the legs or sciatica, mostly combined with insomnia. He thinks that the sciatic nerve is, of all the peripheral nerves, capable of exerting most influence on the nervous centres, and makes a practical induction against the exposure of the limbs, especially in children.

The use of warm foot-baths for relief of congestion in the brain thus finds a more direct explanation than the usual one.

## ELECTRO-MOTOR DISTURBANCES IN THE BRAIN AS PRODUCTS OF PSYCHICAL ACTIVITY.

During 1890 a number of papers bearing on the interesting question as to how far cerebral activity may be estimated by measurement of the electro-motor activity induced in the organ have appeared in the *Centralblatt f. Physiologie*. These independent researches by Professors Beck, Marxow, Gotch and Horsley have induced Prof. B. Danilewsky, of Charkow, to describe experiments undertaken in 1876 for the same purpose, which have nevertheless more than an historic interest.<sup>(2)</sup> The animals were operated on under morphium narcosis by means of unpolarizable glass electrodes, separated by from 10-12 mm., and a very sensitive Du Bois Raymond "multiplicator" served as a galvanometer. In spite of a wide range of variation, the author satisfied himself that "every slightest irritation of the sensory organs, as well as of the inner sensory nerves (vagus), produced an obvious change in the electro-motor state of a definite area of the cortex of the hemispheres (generally the effect is crossed). While it proved impossible to sharply localize these effects, it appeared that stimulation of the sensory nerves of the skin produced a variation in the current in the frontal lobes, while a loud sound affected the occipital region. A pistol shot, for example produced negative variation of 40°.

THE RELATION OF THE SYMPATHETIC SYSTEM TO THE ERECTILE APPENDAGES OF THE HEAD OF THE GALLINACEÆ.<sup>(3)</sup>

In this paper, which gives an illustrated description of the sympathetic system of birds, Prof. Jegorow shows that the vaso-constrictor

1 Soc. de Med. de Paris, 1879.

2 Centralblatt f. Physiologie, V. I, p. 1-4.

3 J. JEGOROW, "Ueber das Verhältniss des Sympathicus zur Kopfversierung einiger Vögel," Du Bois-Raymond's Archiv, 1890, Suppl., p. 33.



fibres governing the erectile vessels in the comb and other analogous appendages arise from the sympathetic system. The fibres supplying the cervical appendages accompany branches of the anterior roots of spinal nerves, while those passing to the head lie in the first and second trigeminal branches. The lids and muscles of the feather papillæ are also supplied by the sympathetic.

#### THE SYMPATHETIC SYSTEM.

In the same line are the observations of Arloing.<sup>(1)</sup> After section of the cervical sympathetic in the case of the ox the corresponding part of the snout became dry and soon began to desquamate. In the case of the dog the effect was not obvious for two months, but then followed the same course.

Recent researches of Doyon<sup>(2)</sup> showed that, while some vaso-dilator fibres of the retinal vessels arise from the sympathetic, others lie in the trigeminus. The author concludes from analogy that the vaso-constrictors are also in the trigeminus. The experiments consisted chiefly in stimulation of the Gasser's ganglion after section of the sympathetic, but without isolation of the ganglion.

By a different method Langley and Dickinson, and later, Langendorff, have endeavored to experimentally determine the function of the cervical sympathetic.<sup>(3)</sup>

#### CONTRIBUTION TO THE STUDY OF THE BRAIN OF TRACHEATE ARTHROPODS.<sup>(4)</sup>

1. *Technique*.—Of several methods of preparation tried, the following was found to yield the best results. After dissecting away the major portion of the insect, the nervous system was hardened in osmic acid, followed by alcohol. The brain was then stained *in toto* with alum or borax carmine.

2. *Histological Elements*.—The arthropod brain is composed of three principal nervous elements: ganglionic cells, nerve fibres and

1 S. ARLOING, "Des rapports fonctionnels du cordon sympathétique cervical avec l'épiderme et les glandes," Arch. de Phys. normale et pathol., 1890, III, 1, p. 160.

2 M. DOYON, "Recherches sur les nerfs vasomoteurs de la rétine et en particulier sur le nerf trijumeau," Arch. de Phys., 1890, III, 1, p. 13.

3 LANGLEY and DICKINSON, "On the Local Paralysis of Peripheral Ganglia, and the Connection of Different Classes of Nerve Fibres with Them," Proc. Roy. Soc., XLVI, p. 423; "The Connections of Peripheral Nerve Cells with the Nerve Fibres which Run to the Sub-Lingual and Sub-Maxillary Glands," Journal of Physiology, XI, p. 123; "On the Progressive Paralysis of the Nerve Cells of the Superior Cervical Ganglion," Proc. Roy. Soc., XLVII, p. 379; "Pituri and Nicotin," Journal of Physiology, XI, p. 265; "Action of Various Poisons upon Nerve Fibres and Peripheral Nerve Cells," Journal of Physiology, XI, Suppl., p. 509. O. LANGENDORFF, "Die Beziehungen der Nervenfasern des Hals-sympathicus zu den Ganglienzellen des oberen Halsknotens," Centralblatt für Physiologie, V, 5, June, 1891, p. 129-131.

4 G. SAINT-REMY, "Contribution à l'Etude du Cerveau chez les Arthropodes Trachéates," Poitiers, 1890, 276 pp., 12 pl., 159 figs.

neuroglia. The ganglionic cells lack a true cell wall, but are surrounded by a sheath of connective-tissue fibres. These cells present various shapes, two of which deserve special mention. One of these types has been called by the author "chromatic cells," the other "ganglionic nuclei." The chromatic cells are small and unipolar, and are confined to the sensory regions of the brain. The bodies of these cells are so poorly supplied with protoplasm that a casual glance reveals nothing but the densely stained nuclei. The higher the type of brain the more numerous these cells become. Among the *Myriopoda*, these cells are very abundant in the complicated brain of *Fulus* and *Scutigera*, while they are absent from the rudimentary brain of *Geophilus*. Among the *Arachnida*, they are abundant in the highly developed optic lobes of the *Lycosidæ* and *Phalangidæ*; in the less differentiated optic lobes of the *Agalenidæ* they are represented by faintly stained cells; while in the rudimentary lobes of *Pholcides* they are replaced by cells of the ordinary type. The ganglionic nuclei are small, granular; densely stained nuclei are found in the brain of *Scutigera*. The nerves are hollow tubes containing a liquid. The tubes passing entad penetrate the brain and expand to form the sheaths of the ganglionic cells. The neuroglia has a more delicate structure in sensory and psychical areas than elsewhere.

3. *Myriopoda*.—The myriopod brain is constructed upon the same plan as the insect brain; it consists of three ganglia homologous to those that are found in the insect brain. Consequently there exists in the myriopods three pre-oral somites homologous to the corresponding somites of insects and crustaceans.

The *protocerebron* (the ganglion of the first cephalic somite) is composed of two portions, corresponding to similar divisions of the insect brain. The lateral portions of the protocerebron constitute the optic lobes, and are in direct communication with the eyes. The remaining portion is psychical in function, and gives off a pair of nerves to the organ of Tömösvary.

The *deutocerebron* (the ganglion of the second cephalic somite) is composed of two antennary lobes, which are united by the antennary commissure, and of an undifferentiated portion, corresponding respectively to the olfactory and dorsal lobes of insects and crustaceans. Except in *Fulus*, where it is divided into an olfactory and probably a motor fasciculus, the antennary nerve is a mixed nerve, as it is in the insects and crustacea. As in the insects and crustacea, so here the dorsal lobe gives origin to a small peripheral nerve (*nerf tegumentaire*), and, as among the insects, it also gives origin to a pair of visceral nerves. Consequently it is homologous to the first paired ganglia of the insects.

The *tritocerebron* (the ganglion of the third cephalic somite) corresponds both to the tritocerebron and to the first visceral ganglion of insects and crustacea. According to Viallanes, the tritocerebron of the crustacea is composed of the following parts: Two antennary lobes, two

œsophageal lobes, and an infra-œsophageal commissure, which traverses the pharyngeal collar. From the antennary lobes a pair of nerves pass to the second pair of antennæ; from the œsophageal lobes nerves pass to the root of the first unpaired visceral ganglion (g. stomato-gastrique) and to the labium. Among insects the third somite and its ganglion suffer great reduction. The somite does not bear appendages, and the antennary nerves, with their lobes, have disappeared. However, the representative of the infra-œsophageal commissure remains. It is united to the brain, and gives off a nerve to each root of the first visceral ganglion and to the labium. From the first visceral ganglion arises an important nerve, which during its course suffers several local ganglionic swellings. In the crustacea this is called the visceral nerve, while in the insects it is called the recurrent. In the *myriopods* the tritocerebrum consists of the same elements as the corresponding portion of the insect brain. In the *Chilognathes* and *Scutigera* the commissure traverses the pharyngeal collar, while in the other *Chilopodes* it is situated in the brain itself. In most families the ganglia consist either of two small bodies situated one at each extremity of the transverse commissure (*Fulides*, *Glomerides*) or of a ganglionic mass situated upon the ventral surface of the commissure (*Scutigeres*, *Lithobiides*). Between these two masses, and isolated from the remainder of the brain, there is a median longitudinal nervous mass, from which arises the visceral nerve. This suppression of the first visceral ganglion and the substitution of a portion of the brain for it is a noteworthy fact. If we admit that the myriopoda are inferior to the crustacea, then this fact warrants the supposition that an isolated visceral ganglion is a secondary feature, and that originally the visceral nerve had its origin in the brain itself. A study of the visceral nerve strengthens this belief. Usually the visceral nerve consists of fine fibres, resembling those of the neuroglia, at whose origin several ganglionic cells are located. In the *Scutigera*, however, this nerve is composed of the neuroglia itself, and contains several nerve cells. It is no longer a nerve, but an elongated ganglion, the homologue of the visceral nervous system of the crustacea and the insects.

4. *Arachnida*.—Among the *Arachnida* the brain consists of three ganglia, corresponding to three somites; but only two of these are pre-oral the third (the mandibular ganglion) is post-oral. The two pre-oral ganglia and their concomitant somites correspond to the first and third ganglia and concomitant somites of the insecta, myriopoda, and crustacea. No trace of a homologue of what constitutes the deutocerebrum of these latter arthropods is found in the *Arachnida*. This implies the absence of the second cephalic somite, the somite which bears the first pair of antennæ of the *Crustacea*, and the antennæ of the *Insecta* and *Myriopoda*.

The optic ganglion is divided into three parts; the optic niduli, the posterior stratified body, and the cerebral niduli. In the *Araneida* the structure of the cerebral nidulus is quite simple, but in the *Scorpionida*

and the *Phalangidæ* it is quite complex. The optic lobe gives origin to a pair of nerves corresponding to one kind of eyes; the nidulus, however, contains two nervous centres, corresponding to two kinds of eyes.

The structure of the rostro-mandibular ganglion is more simple and more uniform. It consists of a nervous mass penetrated by the alimentary canal. The supra-œsophageal portion is composed of three niduli; one small rostral nidulus and two large mandibular niduli. The rostral nidulus lies cephalad to the œsophagus. From it an unpaired median nerve passes to the rostrum. This nerve is the homologue of the nerve that passes to the upper labia of insects, myriopods and crustaceans. The mandibular niduli are laterally situated. They serve to enervate the mandibles. In the *Phalangidæ* there is a single pair of mandibular nerves; in the *Araneidæ*, also, there is only a single pair of nerves, but each nerve is bifurcate; while in the *Scorpionidæ* we find two pairs of nerves.

5. In *Peripatus* the brain is not obviously segmented, but in the remaining tracheate arthropods it is composed of a cephalic and a caudal region. The cephalic portion is pre-oral, and is evidently homologous to both the protocerebrum and the deutocerebrum of insects, myriopods and crustaceans. The caudal region is shown by both embryology and anatomy to be composed of the ganglion of the first post-oral somite. It is probably homologous to the tritocerebrum of insects, myriopods and crustaceans.

6. The roots of the unpaired visceral nerves of myriopods and the paired sympathetic nerves of the *Araneidæ* and *Peripatus* appear to have the same morphological value and to correspond to the unpaired visceral nerves of insects and crustaceans.

7. Among all the tracheate arthropods that possess eyes the first cerebral ganglion contains a more or less differentiated organ (the optic lobes), which is interposed between the deeper regions and the retina. Its function appears to be the elaboration of visual impressions. The structure of this organ is not necessarily constant for the same kind of eye, and variations in its structure apparently greatly modify the phenomena of vision. Indeed, modifications of this body appear to be of more importance than variations of the eye itself. The remainder of the cerebral ganglion is not entirely concerned with vision; it is psychical in function. The structure of these regions is greatly influenced by their physiological rôle.

[C. H. T.]

#### THE NERVOUS SYSTEM OF COPEPODS.<sup>(1)</sup>

The brain of *Diaptomus*, according to this author, is an irregular body, consisting of a central mass of "dotted substance" surrounded by a layer of cells, varying in thickness at various points. The primary brain consists chiefly of "dotted substance," the secondary of nerve

1 M. J. RICHARD, Bull. Soc. Zool. France XV, 1891.

cells. Nerves arise from the brain for the frontal organ, eyes, first pair of antennæ and the labrum. This supra-œsophageal ganglion is united by strong connectives with the sub-œsophageal, and the connective is supplied with scattered cells laterad. Nerves are given off from it to the second antennæ and labrum. A number of ganglia are united in the band-like sub-œsophageal mass. Three tuberosities correspond to mandibles, maxillæ and maxillipedes. There are regular blood sinuses or lacunæ extending through the system. All the nerve cells are of the multipolar type.

#### THE DEVELOPMENT OF THE NERVOUS SYSTEM OF SPIDERS.<sup>(1)</sup>

This Japanese author has investigated especially the development of the eyes, using the genera *Agalena* and *Lycosa* principally, and verifying statements by comparison with *Theridion*, *Epeira*, *Dolomedes* and *Pholcus*. His statements conflict with those of Locy, Schimkewitch and Patten in several particulars. Segmenting stages of the eggs were plunged directly into hot water, while older eggs were gradually heated in water to 70 or 80° C. The process was continued until the eggs were opaque and white. After cooling they were placed in 70 per cent. alcohol and carried up to absolute gradatim. The precaution was taken of examining the eggs one by one under a dissecting microscope and all those in which the membrane was not burst were perforated by a needle to facilitate permeation. They were stained in alcoholic cochineal, picrocarmine, alcoholic carmine and hæmatoxylin. Paraffin was the imbedding agent.

The following statements from the author's summary are germane to our work:

The brain and the ventral nerve cords are formed as a continuous ectodermal thickening. The brain is composed of the semicircular grooves and the lateral vesicles cut off from the ectoderm. Later it is divided into three segments. The development of the posterior median eyes is connected with that of the brain. Their development is quite different from that of the other eyes; but all the eyes are dermal in origin, not neural, and the nerves of the eyes always enter from the inner ends of the ectoderm cells.

The spider's brain consists of three segments, as Patten claims. From his description, Patten seems to mean that in scorpions and spiders the three segments of the brain are formed from three separate invaginations; but I am unable to corroborate this statement. Moreover, he says that the anterior median eyes (my posterior median) belong to the second segment, while the three remaining pairs belong to the third segment. Supposing that his second segment is anterior to the third segment, I cannot corroborate this statement either,

<sup>1</sup> KAMAKICHI KISHINOUE, "On the Development of Araneina," the Journal of the College of Science, Imperial University of Japan, Vol. IV, Part I, pp. 55-88, Plates XI-XVI.



as, according to my observations, all the eyes belong to the third segment.

The concentration of the nervous system toward the cephalothorax continues until the lateral ganglionic chains are united into one and form the sub-œsophageal ganglion. The inner portion of the ganglion becomes finely fibrous. The abdominal ganglia gradually atrophy and attach themselves to the posterior end of the sub-œsophageal ganglion.

The plates are well executed, though lacking in detail.

#### NERVOUS SYSTEM OF SERPULA<sup>(1)</sup>.

"The nervous system is quite highly developed, the cerebral ganglion attaining a diameter of .5 mm. in specimens whose whole body diameter was 1.4. This ganglion gives off, in front, two large branchial nerves, which supply the branchiæ and two smaller nerves to the œsophagus. A single nerve from its posterior, ventral, median edge runs to the posterior part of the œsophagus.

The cerebral ganglion gives off, on either side, a large commissure, which passes down around the œsophagus and into the large ventral ganglion of the corresponding side." The ventral chain continues through the entire body with a ganglion for each segment. The sub-œsophageal ganglion has three transverse commissures, and the others which decrease backward have but one. About two-thirds of the mass of the cerebral ganglion is made up of cells, while the inner portion is composed of fibres. The other ganglia contain but few cells, arranged on the outer surface.

"At its posterior end, the dorsal portion of the cerebral ganglion is prolonged into a most remarkable process; from the dorsal, posterior corner on either side a large lobe passes outward and backward, and then, bending suddenly downward, passes into the first ventral ganglion. It will be seen that we have here, in reality, two pairs of œsophageal commissures."

#### DEVELOPMENT OF THE BRAIN OF THE HORSE-SHOE CRAB.<sup>(2)</sup>

"The nervous system arises from a paired, longitudinal thickening of the ectoderm. The anterior ends of these thickenings are much broader than the posterior parts, and there are two pairs of ectodermic invaginations. These parts form the brain. About twenty-four days after fertilization nine pairs of ganglia may be seen (there is a pair in the metastoma). They are separated from the general ectoderm from the anterior end gradually. From the third pair of ganglia, backwards, there is a lateral commissure in each segment. The brain has one transverse commissure.

<sup>1</sup> TREADWELL, A. S., "Preliminary Note on the Anatomy and Histology of *Serpula Dianthus*," Zool. Anz., XIV, 370, p. 276.

<sup>2</sup> KISHINOUE, K., "Preliminary Note on the Development of *Limulus Longispinis*," Zool. Anzeiger, XIV, 369, pp. 264-266.

The separation of the brain from the general ectoderm is later than that of ganglia. There is a peculiar grouping of the nuclei, as that found in the retinal portion of the eye, in the nervous system before it is separated from the general ectoderm."

#### BRAIN OF THE HORSE-SHOE CRAB.<sup>(1)</sup>

The brain of the adult is made up of three pairs of lobes, enveloped in thick masses of chromatic cells. The uppermost are the pair of lateral eye lobes, widely separated from each other on the top of the brain and give off well-developed nerves.

The nerve cells appear to arise from the chromatic cells. "The lobe just below the middle is seen to be imbedded in the dense ring or ruffle-like masses of deeply-stained chromatic cells, which we have called the 'nucleogenous bodies.'" The brain of *Limulus* differs from that of *Arachnida* in sending no nerves to the first appendages, and is homologous with the forebrain of spiders, according to Patten. "The nerves which give rise to the first pair of appendages do not arise from the base of the brain, but the ganglion cells giving rise to them are situated entirely outside of and behind the brain proper." The lobes of the median-eye nerves are small and slender and not much swollen, and lie far below [ventrad of?] the plane of the lateral-eye lobes. Their form and size indicate that they have atrophied.

There is, below the median-eye lobes, a pair of minute lobes, each sending off a bundle of fibrillæ backward [caudad?] toward the cerebral commissure, which may possibly give rise to a pair of tegumental or hæmal nerves. No traces were discovered of Patten's nerves of the median eye of the first segment."

The third pair of (major) lobes are the cerebral lobes. These are very irregular in outline, slender and apparently shrunken, and very different from the full well-developed sub-spherical shape of those of arachnids.

Prof. Packard differs from Viallanes in believing that there are "but three preoral segments of the head" of insects. He considers that the differences are of sufficient importance to forbid the union of the *Podostomata* with the arachnids.

#### EDINGER'S TEXT-BOOK ON THE NERVOUS SYSTEM.<sup>(2)</sup>

It is a pleasure to note the publication in this country of a condensed manual of the anatomy of the human brain by so eminent an investigator as Dr. Edinger. It is equally pleasant to note that the

<sup>1</sup> PACKARD, ALPHEUS S., "Farther Studies on the Brain of *Limulus Polyphemus*," Zool. Anzeiger, XIV, 361, pp. 129-133.

<sup>2</sup> EDINGER, LUDWIG, "Twelve Lectures on the Structure of the Central Nervous System, for Physicians and Students" Second revised edition, with 133 illustrations. Translated by WILLIS HALL VITTUM; edited by C. EUGENE RIGGS Philadelphia: F. A. Davis, 1890.

translator and editor are connected with the newly equipped medical department of the University of Minnesota. That the student of anatomy at this institution may now avail himself of the ripest fruit of German scholarship is a matter of congratulation to alumni of that institution, who, like the writer, recall a very different state of things.

The book itself is familiar to students of neurology in the earlier edition. The improvements introduced in the second edition are important, and in most, though not all, respects it represents fairly the present state of our knowledge. The translator and editor are to be congratulated on their share in the work. The originally clear style is rendered into perspicuous English with little of the awkwardness often attending a translation. It is a wholesome symptom that in descriptions involving direction the reformed terminology is employed, and we may soon hope to escape from the ambiguous "back," "above" and "inward" of anthropotomy.

The figures, which are numerous and excellently adapted to the purpose, suffer somewhat in reproduction; but there is, perhaps, a decided gain in the fact that the original German terms are printed *in situ*, preventing ambiguity and affording an opportunity for becoming familiar with the indispensable nomenclature in its mother tongue. A few, like Fig. 83, are useless by reason of careless neglect of reference lines. Many who consult the work will regret its brevity, but these will not be those for whom it has obviously been written—medical students. The book is a text-book, and we must admire the self-control exercised by the author in omitting doubtful points, even where he himself is personally interested in a militant theory. One thing we greatly miss; a detailed description of a few of the modern technical methods would greatly extend the value of the work for Americans who have no handbook of neurological technique. We hope the next edition may be provided with an appendix containing sufficiently minute technical recipes and directions.

It would be easy to point out omissions and cases where the author's statements conflict with the results of recent investigation, but in a science which is advancing as rapidly as the present one this is inevitable, and something must be granted to private judgment. If the treatment of the cephalic cranial nerves is less satisfactory than other portions, the cause is not far to seek in the nature of the subject. On the whole, there is no other work which occupies this important field so satisfactorily.

#### MYOCLONUS.

While strictly beyond our limits, the recent pathological work of Unverricht<sup>(1)</sup> may be mentioned as a model of thoroughness and discrimination in an exceedingly different realm. The disease known as

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1 UNVERRICHT, H., "Die Myoclonie," Leipzig and Vienna, Franz Deuticke, 1891.

paramyoclonus multiplex was described by Friedreich in 1881, with symptoms such as clonic contractions in a number of symmetrical muscles of the extremities, without affecting the normal coördination and reaction of the muscles otherwise. Reflexes were abnormally sensitive. A fright or other psychical cause is claimed for the disease, which may be spontaneously self-limited. The author cites a number of very instructive cases showing that it may assume the congenital phase, and apparently succeeds in effecting a differential diagnosis. The prognosis is as unpromising as the theropathy unsatisfactory.

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## LITERARY NOTICES.

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### DEGENERATION OF PERIPHERAL NERVES.<sup>1</sup>

In 1795 Cruikshank divided the vagus-sympathetic nerve trunk in the neck of a dog and found that, when the section was performed on both sides, death followed very promptly, while a unilateral section was not fatal. He then divided the nerve on one side and, after an interval of three or more weeks, cut the other. The animal survived, thus showing that the severed trunk had meanwhile united. This experiment seems to have been the starting point for a long series of research upon the nature of the dependence of nerve fibres upon nerve centres, which have culminated in the masterly monograph before us.

Flourens (as it is claimed) succeeded in suturing the cut ends of the median and ulnar nerve, each to the stump of the other. Functional union was effected and stimulation of the dorsal nerve caused motion of the ventral peripheral muscles and *vice versa*. Since Flourens' time the fact that a severed nerve may again become functional has been repeatedly demonstrated, but it has not been so easy to determine whether the union was preceeded by a degeneration and regeneration of the entire peripheral portion. The histological problems involved, *e. g.* whether the axis cylinder repenetrated the sheath from the stump, have remained unsolved.

When the nerve is cut and the stumps not reunited or sutured, every one admits that a process of degeneration follows. Beyond this there is little unanimity. All admit that the myelin disappears, but Neumann, Eichhorst, Mayer, etc., suppose that the myelin simply suffers transformation and forms the material of the new sheath in case of regeneration. While some describe the process of degeneration as beginning at the proximal end, the majority recognize the process as coetaneous through-

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<sup>1</sup>1. HOWELL, W. H. and HUBER, G. C. A Physiological, Histological and Clinical Study of the Degeneration and Regeneration in Peripheral Nerve Fibres after severance of their connections with the nerve centres. *Journal of Physiology*, XIII, 5, 1892.

out the peripheral portion. Earlier writers suppose that the axis cylinder remains intact. Neumann and Eichhorst believe that it suffers transformation without actually disappearing, but most writers describe its disappearance with the sheath structures. The belief that a nerve fibre is an outgrowth of a cell in the central system (often several feet long!) has contributed to produce a predisposition to a belief in the degeneration as a result of trophic disturbance. Great difference of opinion exists as to the possibility of a union by first intention. Some cases in which, after suturing a nerve, there was almost immediate restoration of function seem to sustain such a view.

The paper above noticed contains abundant historical matter and a full list of titles. The work of the authors themselves has been largely experimental, but in all cases the results have been elaborately checked and enlarged by histological investigation, thus giving to the results obtained a degree of precision which cannot be too highly commended. Dogs were used in the experiments and the ulnar, or ulnar and median nerves were selected. Operations were carried on with antiseptic precautions and the nerve fibres were sutured with carbolized catgut or catgut in juniper oil. Two sutures were used, one on each side, the needle being passed through the epineurium. Continuity of the nerve was destroyed by section with sharp scissors, crushing by a ligature, or coagulation by means of a current of water at 80 degrees C. passing through a curved glass tube. Morphia and ether were employed as anæsthetics. The testing stimulus was a unipolar electric current, the indifferent electrode being applied over the skin of the sternum. In some cases a small block of hard rubber was passed under the nerve and a direct impact employed as stimulant.

1. In none of the cases was there union by first intention, the peripheral end degenerating throughout its whole extent.

2. The time necessary before loss of irritability and conducting appears, varies greatly (between 2 and 4 days.)

3. The return of function readily but gradually takes place if the ends are primarily sutured.

4. The irritability returns first in the vicinity of the wound. It only returns when regeneration has proceeded so far that some medullated fibres are present.

5. The return of function takes place more quickly in sensory than in motor fibres. This is explained by the authors as due to the greater



difficulty of affecting connections (in the end-plates of muscles, for example.)

6. Light mechanical stimuli were often more effective in exciting the fibres in an early stage of regeneration than electrical induction shocks. [May this not be due to the greater autonomy of the segments and the functional activity of the local elements during this stage?—ED.]

7. Conductivity is restored before irritability; but these embryonic fibres respond to mechanical impulse when not to electric shock. [See remark above.]

8. The possibility of the functional union of two spinal nerves was proven. The central end of the median was united to the peripheral end of the ulnar nerve and the peripheral stump of the median and the central stump of the ulnar were dissected away. Functional union occurred and the animal was examined after 75 days. The physiological results of the union were unfortunately poorly differentiated.

In the histological study the best results were obtained by the method of teasing. The fresh nerve was pinned out, hardened and stained in osmic acid 24 hours, then washed in water 24 hours or six to seven days. Next it was partially teased, stained in Bœhmer's hæmatoxylin and examined by teasing on the slide in glycerine or Farrant's solution. Other nerves were hardened in Mueller's fluid, then, after partial teasing, were stained by Freud's potash-gold method and treated with hæmatoxylin for nuclei. This method brings out the axis cylinder. A third method is recommended, which consists in pinning out in picric acid, saturated solution, 48 hours. They were then washed out in water 5 or 6 hours and subsequently in 33 and 50 per cent. alcohol and preserved in 95 per cent. They were then partially teased and stained 10-15 minutes in Bœhmer's hæmatoxylin. The process seems to expose the axis cylinder by removal of the myelin.

"After the interruption of the connection between a nerve fibre and its centre, whether the interruption be by actual section, by crushing, or by coagulation, the peripheral end of the fibre undergoes degeneration, the changes affecting first the myeline and the axis, and subsequently the sheath and its nuclei." The degeneration begins, in the dog, after about 4 days. The fragmentation of the myelin sheath (at the lines of Lantermann) is regarded as independent of and prior to the increase of protoplasm about the nuclei. The axis cylinder breaks up with the myelin

and remains enclosed within the latter. These changes take place substantially cotemporaneously throughout the peripheral end. A secondary fragmentation occurs first in the vicinity of the nuclei. By the seventh day there is active proliferation of the nuclei. After subdivision the nuclei migrate and set up new centres of absorption.

Regeneration begins with the formation of new protoplasm about the nuclei, which then assume the form of bipolar cells; at a later period the whole sheath is filled with a continuous belt of protoplasm in which the nuclei are imbedded. Such a fibre is called an embryonic fibre by reason of its resemblance to the early condition. In some cases it appears that two new fibres may be formed in one old sheath.

In case the cut ends are not united, regeneration never gets beyond the embryonic stage. If united the myelin is formed discontinuously, generally near the nucleus, subsequently uniting to form a continuous sheath. Respecting the nuclei, the authors are not clear. They suppose that they disappear by absorption.

"With reference to the nodes and internodes of Ranvier, it is evident that no simple hypothesis, such as the development of each internode from a single cell, will fit the facts as they appear in regenerating fibres." They admit that the internodal nucleus must, throughout life, play an important part in the nutrition of the protoplasm in connection with it and of the myelin sheath. "In an indefinite way we may suppose that this nutritive influence on the myeline can only extend over a limited area—the distance of an internode,—but to connect this with the formation of these internodes takes us into the field of speculation, though it seems to us that the true explanation lies along this line of thought. The origin of the segments of Lantermann may doubtless be traced directly to the primitive, disconnected deposits of myeline which we have described." The authors seem to believe that the axis cylinder proceeds from the stump into the newly formed myelin, a position rendered very improbable by their figures.

"In the central end, especially when connection with the periphery is not made, several new fibres may form within the sheath of an old one to take the place of the portion degenerated. Each of these may develop myeline and receive a branch from the axis cylinder above."

The paper is a credit to American science and it is a great pity that it should not have found an American medium of publication. The plates are exceedingly instructive.

We cannot forbear adding that the obvious influence of a strongly supported histogenetic hypothesis has been a serious detriment to the theoretical portion of the work. Even our elementary text books teach that the peripheral nerves are formed as the outgrowths of a single central cell. Such outgrowths being, accordingly, in some cases, several feet long (Martin's Human Body.) So far as can be gathered, this is pure assumption and is inherently very improbable. Study of the growth of nerves in embryos of serpents, amphibians and mammals, has convinced the writer that, in some cases at least, the growth is by moniliform adhesions of neurons. The process is essentially the same as that occurring in the tracts of the cord where the longer reaches of tracts are in like-manner thus formed. When definite functional paths are formed the nuclei are relieved of part of their function and a variety of subsidiary processes resembling fatty degeneration occur, and in this way sheaths are formed. The case of the olfactory is therefore simply a striking illustration of the normal process which is less clearly seen elsewhere. If this be accepted, it may be admitted that the effect of a proliferating nerve upon the developing adjacent tissues may for a time be less dependent on the central than the peripheral neurons.

It is not a little strange that a second work covering the same ground, with similar methods should appear at nearly the same time.<sup>1</sup>

This paper was awarded the medical prize of the Faculty of Würzburg University for 1891.

The author's summary is substantially as follows: After an injury to a peripheral nerve destroying its substance at any point, the entire peripheral portion, as well as a short part of the central stump, degenerates. Healing by first intention does not occur. The degeneration of the immediate vicinity of the wound is followed, 48 hours after, by a paralytic degeneration of the peripheral part, which is due to various causes. The axis cylinder gives up fluid and grows smaller. Its shrinking produces fragmentation of the sheath. The contraction of these fragments produces a corresponding rupture of the axis. At about the fourth day the nuclei of Schwann's sheath begin to proliferate and the protoplasm increases, which process perhaps assists in the degeneration. The

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1. NOTTHAFT, A. F. N. Neue Untersuchungen ueber den Verlauf der Degenerations- und Regenerationsprocesse am verletzten peripheren Nerven. Zeitsch. f. wiss. Zool., LV, 1. Nov., 1892.

degenerating medullary sheath leaves a fluid in the sheath which is gradually absorbed. There is not a fatty degeneration of the medullary sheath, though infiltration of fat in adjacent structures cannot be denied. Neither is there a chemical transformation in the sense of Neumann and Eichhorst. Leucocytes have nothing to do with the degeneration, and Ranvier went too far in ascribing it solely to the proliferation of the nuclei. The axis cylinder decomposes before the medulla and sheath. The degeneration passes with marvelous speed from the site of injury peripherad.

The proliferating nuclei of Schwann's sheath seem to facilitate the degeneration and regeneration, but neither they nor the increased protoplasm have anything to do with the formation of the axis cylinder. Bünger's protoplasm bands are probably simply folds in Schwann's sheath. There is no reason to doubt the statements of Koelliker as to the consistency of the axis cylinder and the connective nature of the sheath. The axis cylinder grows from the central stump continuously. The new fibres appear in 8 or 10 days. In some cases the medullary sheath is not at once formed. Nerves caused to degenerate by crushing do not form more than a single fibre in a sheath. The new Schwann's sheath is apparently formed by the nuclei of the old sheath.

To judge from the drawings there is much reason to suspect that a better interpretation would show an intimate connection between the nuclei of Schwann and the axis cylinder, which latter is jointed in a way suggestive of moniliform conrescence.

#### THE CEREBRUM OF REPTILES.<sup>1</sup>

This extensive paper by a young physician recently Americanized contains promise of good work, but fails of adding materially to our knowledge by reason of ignoring previous writers and the crude methods employed. The terminology is that of Edinger. Brains hardened in Mueller's fluid and stained with analine cannot be expected to yield histology. The differentiation of cells seems to have been imperfect, but the difference between the pyramidal and fusiform cells of the various areas were made out. Although special attention is given to the snake brain we find no mention of the remarkable peculiarities of the tuber with its lateral peroneal and olfactory fossa and no recognition of the relation

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1. MEYER, A. Ueber das Vorderhirn einiger Reptilien. Zeitsch. f. wiss. Zool. 1

between *pero* and *pes*. Although strongly criticising the misuse of anthropotomic terms he employs *septum* and *nucleus sphericus* contrary to the law of priority.

It is hoped that the author may continue his studies and extend the present publication, which will be critically discussed in another place.

#### IS THE RETENTION OF URIC ACID PATHOGENETIC OF NERVOUS DISEASE?<sup>1</sup>

This paper contains much of great value to the physiologist and pathologist. The methods of determining uric acid and urea, physiological variations in the excretions, quantitative relations of urea and uric acid in health, influence of drugs, etc., are treated critically as preliminary to the question of the excretion of uric acid in disease.

The authors devote considerable space to the criticism of Haig's theories that certain kinds of food render the blood less alkaline and thus occasion a storing up of the uric acid (which is more soluble in an alkaline solution) in the tissues. When the blood becomes more alkaline an excess is thrown into the blood, producing migraine headache, epileptic paroxysm or mental depression. A general criticism of this view rests on the scantiness of evidence adduced. The theory of storage of uric acid is regarded as inherently improbable. The authors observe increase of uric acid excretion in chorea, proportional to the severity of the attack. With respect to epilepsy the authors say, "We may, however, say that we have as yet obtained no grounds for the view that the *grand mal* paroxysm of idiopathic epilepsy is regularly or even usually preceeded by diminished uric acid excretion."

The increase follows the paroxysm, being often greatest on the second day, which fact may be supposed to suggest that the uric acid increase is due to conditions associated with, or perhaps occasioning the attack. *Petit mal* cases exhibit a large and persistent excess.

Paroxysmal vomiting in children is often followed by a very remarkable increase and migraine shows a considerable increase. It is concluded that the increased excretion is an effect of numerous different derangements of nitrogenous metabolism.

A second paper by the same authors<sup>2</sup> discusses these questions fur-

1. HERTER AND SMITH. Observations on the Excretion of Uric Acid in Health and Disease. N. Y. Med. Journ., June 4, 1892.

2. Researches upon the Aetiology of Idiopathic Epilepsy. N. Y. Med. Journ., Aug.-Sept., 1892.



ther and seems to indicate some connection between intestinal putrefaction and epilepsy. The evidence on this head is interesting but far from convincing.

#### EXCISION OF CORTEX AS A CURE FOR INSANITY.<sup>1</sup>

Six cases of chronic mania, dementia, etc., were operated by removal of 2 cm. or more of the cortex, the areas corresponding to the seat of the sense chiefly affected by hallucination. In five cases, amelioration, in one, death resulted. The effect seems to consist in the transformation of impulsive mania into passive dementia, frequently with removal of the hallucinations.

#### JAMES BRIEFER COURSE IN PSYCHOLOGY.<sup>2</sup>

Professor James is a teacher, and his much used work is conceived as only a teacher could. It contrives to supply very much of the vivacity and piquancy of personal instruction within the compass of a text book. Add to this the fact that he is especially alive to the prevailing tendencies in psychological thought and we have a partial explanation of the sudden success of a work which is neither logical in arrangement nor faultless in psychical analysis. The briefer course seems to us a vastly more usable book. The author describes it as three-fifths "scissors and paste." These three-fifths have greatly gained, from the student's standpoint, through both these modifying agents. The scissors have relieved him of tapestries which would, in all probability have hung in shreds about his hurrying feet, and the paste has been "mixed with brains." The two-fifths not accounted for supply important physiological details as to the sensory organs which American classical courses seem never to adequately supply in the term or two of physiology.

Many teachers will object to building up the fabric of an elementary text-book upon such a 'working hypothesis' as this: "Mental action may be uniformly and absolutely a function of brain-action, varying as the latter varies, and being to the brain as effect to cause." Conscious processes are divided into sensation, cerebration, and tendency to action.

The paragraphs on sensation fail to distinguish adequately sensation and perception. Especially unsatisfactory is the discussion of external-

1. BURCHARDT, G. Allg. Zeitsch f. Psychiatrie, XLVII.

2. JAMES, WILLIAM. Psychology, American Science Series. Briefer Course. Henry Holt & Co., New York, 1892.

zation and excentric projection. The author claims that "the very first sensation which an infant gets *is* for him the outer universe." "The object which the numerous impouring currents of the baby bring to his consciousness is one big, blooming, buzzing confusion. That confusion is the baby's universe." Many such expressions make us wish that the author could have escaped from some of the consequences of the contact with American tendencies which nevertheless impart the breeziness of style which compel almost unwilling admiration. The chapter on the structure of the brain, supplemented by that on its functions, gives a synoptical sketch of the neurology, and it is the teacher who says, with a sigh perhaps, "When is all is said and done, the fact remains that, for the beginner, the understanding of the brain's structure is not an easy thing. It must be gone over and forgotten and learned again many times before it is definitely assimilated by the mind."

The chapter on habit is full of useful maxims. Many will gratefully agree that "the traditional psychology talks like one who should say a river consists of nothing but pailsful, spoonsful, quart pots full, barrels full and other moulded forms of water;" and accept with such grace as he may the conclusion that "each of us dichotomises the Kosmos in a different place."

The chapter on attention is especially good. James adopts (with regret) the terms *recept* (or *construct*) and *isolate* of comparative psychology. He goes the full length of Professor Bain in assuming that all consciousness is motor according to a law of diffusion. "A process set up anywhere in the centres reverberates everywhere, and in some way or other affects the organism throughout, making its activities either greater or less." James follows Lange in asserting that "bodily changes follow directly the perception of the exciting fact and that our feeling of the same changes as they occur *is the emotion*." While not wishing to belittle the physical concomitants in emotion, we protest that it is a pity to strip these important sections of our psychical life of their cognitive elements. It seems to us that James has fallen into an error analogous to those against which he has warned us. In classing emotions as a variety of impulses, as in the earlier work, he prepared the way for this error. A more natural order is here followed, viz: (1) Expression of emotion, (2) Instinctive or impulsive performances, (3) voluntary deeds. We object to identifying emotion with either its expression or physiological element. No doubt many emotions are due to reflexes producing total sen-

sations, but such sensations have this as a characteristic that they implicate the empirical ego, and that act of cognition which forms the nexus between the physical shock and the subject of consciousness can no more be left out than the data of effort can be left out of perception.

The chapter on will is quite a full reproduction of that in the larger work and is so suggestive that no attempt can be made to discuss it here. The work has that prime requisite of a text book, it is suggestive and fresh and does not leave the student with the deadly delusion that he has finished the subject.

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